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Helmut Berger

Monograph of the Gonostomatidae and Kahliellidae (Ciliophora, Hypotricha)

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Monograph of the Gonostomatidae and Kahliellidae (Ciliophora, Hypotricha)

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Dedication

This book is dedicated to my friend and colleague Weibo Song from the Ocean University of China (OUC; Qingdao, China). Weibo made the OUC to an acknowledged centre of ciliate taxonomy and is author of many important works on the systematics of hypotrichs, especially from marine habitats.

Preface

The present book is part four of the Monograph of the Hypotricha, a series which reviews in great detail this highly interesting group of spirotrichous ciliates. The monograph is the most extensive revision since Kahl (1932), which is still an important treatise. The series will comprise six volumes.

The first volume is about the oxytrichids, a group which was considered for a long time as monophyletic because of the rather stable pattern of 18 frontal-ventral-transverse cirri (Berger & Foissner 1997, Berger 1999). However, the many molecular analyses published in the last decade combined with the sifting of the morphological and ontogenetic data indicate that this conspicuous pattern very likely already evolved in the last common ancestor of the Hypotricha so that it cannot be used as apomorphy of a subgroup of the hypotrichs (Berger 2006a, 2008). Now, I consider the fragmentation of dorsal kinety 3 as main morphological apomorphy of the oxytrichids (Berger 2006, p. 33; 2008, p. 46). Consequently, "18-cirri hypotrichs" which lack this fragmentation are very likely misplaced in the oxytrichids, for example, *Gonostomum*, *Urosoma*, *Urosomoida*, or some *Oxytricha* species (e.g., *O. lanceolata*). The misplacement of *Gonostomum* in the oxytrichids is also shown by molecular data, indicating that the dorsal infraciliature is as important as the ventral cirral pattern for the estimation of the major phylogenetic relationships within the hypotrichs.

The second volume of the series is mainly about the Urostyloidea (Berger 2006a), a rather large group whose members have the urostyloid midventral complex (zigzagging frontoventral cirri originating from more than six anlagen) in combination with the simple, plesiomorphic dorsal kinety pattern composed primarily of three bipolar bristle rows. Thus, species which also have a zigzagging cirral pattern, but a more complex dorsal infraciliature (e.g., dorsal kinety 3 fragmentation and/or dorsomarginal kineties) have been removed from the urostyloids, for example, *Neokeronopsis* and *Uroleptus*. The latter genus is now assigned to the so-called Dorsomarginalia (Berger 2006a), where it branches off rather basally. By contrast, *Neokeronopsis* belongs to the oxytrichids – a large subgroup of the Dorsomarginalia – because it has the same type of dorsal kinety fragmentation (Berger 2006a, p. 1190). This hypothesis was later corroborated by molecular data (Foissner & Stoeck 2008).

The Amphisiellidae and Trachelostylidae are the major taxa treated in the third volume (Berger 2008). The amphisiellids (e.g., *Amphisiella*, *Lamtostyla*, *Hemisincirra*) are non-dorsomarginalian hypotrichs with a more or less prominent frontoventral row formed from two or three anlagen, while the trachelostylids are a small group of marine 18-cirri hypotrichs with a curious dorsal kinety pattern, at least in the type species of the whole group. In addition, several genera of uncertain or unknown position within the hypotrichs have been included, for example, *Apourosomoida*, *Erimophrya*, or *Hemiurosoma*. Two species previously classified in *Hemisin-*

cirra have been transferred to the urostyloid genus *Anteholosticha* for which a new key was added.

The present volume is about the Gonostomatidae and the Kahliellidae. *Gonostomum*, the name-bearing type genus of the Gonostomatidae, was previously assigned to the oxytrichids because the type species *G. affine* is basically an 18-cirri hypotrich (Berger & Foissner 1997, Berger 1999, see also second paragraph of present preface). We hypothesised that the simple dorsal kinety pattern – three bipolar kineties with caudal cirri – has evolved from the complex oxytrichid pattern by a loss of both dorsal kinety fragmentation and dorsomarginal kineties. Molecular analyses however indicated that *Gonostomum* branches off rather early in the Hypotricha tree. This supports the hypothesis that *Gonostomum* has taken over the simple dorsal kinety pattern from the last common ancestor of the hypotrichs (Berger 2008, p. 23). An important morphological apomorphy of the gonostomatids is the conspicuous oral apparatus: the major portion of the adoral zone extends mainly along the left body margin while the proximal portion curves knee-shaped towards cell midline. In addition, the paroral is composed of few to very few, rather widely spaced cilia. This pattern also occurs in some other genera, for example, *Paragonostomum*, *Wallackia*, and *Cladotricha* so that the reactivation of the Gonostomatidae Small & Lynn, 1985 seems useful. Further studies will show whether or not this was an equitable decision.

The kahliellids are a difficult, uncertain group because a strong apomorphy is lacking. Currently, the preservation of parental structures (e.g., marginal rows, dorsal kineties) in the next generations is used as unifying feature. In addition, the type species of the whole group is relatively little known so that the present review is certainly only an interim solution. Molecular data about "kahliellid" species are rare and do not support, as in many other cases, the morphological classification.

Most taxa reviewed in the present book are terrestrial and/or limnetic, that is, very few (e.g., *Pseudokahliella marina*) are marine. Only few species, for example the very common and widely distributed *Gonostomum affine*, are known for a long time (Stein 1859). Most have been discovered in the 1900s by Kahl, Horváth, Ruinen, Foissner, and Eigner. Thirty-three gonostomatids, 15 kahliellids, and 24 "other" species are reviewed as valid in the present volume. Details about synonymy rates will be provided in the last volume of the monographic series.

As in the previous volumes, almost all available data on morphology, ontogenesis, molecular biology, ecology, and faunistics have been included. For each species, a detailed list of synonyms is provided, followed by a nomenclature section. In the remarks, all important data concerning systematics, synonymy, phylogeny, and similar taxa are discussed. The morphology section contains a thorough description, following the same sequence in every species. If the data on various populations or synonyms do not agree very well, then they are kept separate so that even workers who do not agree with the synonymy proposed can use the revision. For several species, cell division data are available. They are also included because the ontogenesis is often very important to understand the interphasic cirral pattern correctly. The oc-

currence and ecology section contains a description of the type locality and all other localities where a species was recorded. In addition, almost all illustrations published so far have been included. Thus, with the present book the general microscopist need not refer back to the widely scattered original literature. Specialists, however, should always check both the present treatise *and* the original description or authoritative redescription when redescribing a known species.

The next major group which will be treated is the renowned, but difficult genus *Uroleptus*. As already mentioned above, *Uroleptus* has been assigned to the urostyloids previously because both have zigzagging ventral cirri. However, they differ distinctly in the dorsal kinety pattern (dorsomarginal row present vs. absent) and the gene sequences, indicating a convergent evolution of the so-called midventral pattern. Only recently, Foissner & Stoeck (2008) established the Uroleptidae, which comprise mainly limnetic and terrestrial species. Probably, volume 5 will also contain the Keronopsidae, a relatively small group characterised, inter alia, by a dividing cyst.

As already discussed in the preface to the amphisiellids and trachelostylids, I will certainly find already known species which should have been reviewed in a previous volume. Such taxa will be treated in supplements at the end of each book, as already done in Berger (2006a, 2008) and the present revision (*Apourosomoida*). The last volume of the monographic series will contain a key and a systematic index to all species so that the user can find all hypotrichs very easily within the various volumes.

The Republic of Austria generously supported the monographic series via the Austrian Science Fund FWF and the Austrian Academy of Sciences, and I hope so that this will continue until the series is completed, in spite of the banking crisis.

Salzburg, August 2010 Helmut Berger

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Contents

A General Section

The following chapters deal with the general external and internal morphology of the Gonostomatidae (= gonostomatids)[1] and the Kahliellidae (= kahliellids), and terms specific to these taxa are described and explained. For general terms see also the corresponding sections of the previous volumes (Berger 1999, 2006a, 2008), especially Fig. 6a, b in Berger (1999), Fig. 1c, d, f, g in Berger (2006a), and Fig. 1a–h, 7a, b in Berger (2008). However, the illustrations of the individual species described in the systematic section are labelled in great detail so that even inexperienced workers will understand the morphology easily in most cases. For explanation of other terms, see Corliss (1979), Corliss & Lom (1985, 2002), Lynn & Corliss (1991), Hausmann & Bradbury (1996), Hausmann & Hülsmann (1996, 1996a), Hausmann et al. (2003), Fokin (2007), and Lynn (2008). The (supposed) ground pattern of the Hypotricha is discussed in detail in the phylogeny chapter of Berger (2008, p. 23). For comments on the ground pattern of the kahliellids and gonostomatids see the systematic section. Other topics, namely phylogeny, previous classifications, parasitism, ecology and distribution, and methods, are briefly discussed in chapters 2 to 6. In chapter 7 the applied species concept is briefly discussed and the nomenclatural acts are summarised.

1 Morphology, Biology, and Terminology

1.1 Size and Shape

Gonostomatids and kahliellids are usually moderately small or medium-sized, that is, the majority of the species is between 60 µm and about 200 µm long. The largest species treated in the present volume are *Circinella arenicola* (200–600 × 18–30 µm), *Saudithrix terricola* (200–350 × 70–150 µm), and *Engelmanniella mobilis* (170 to 270 × 18–23 µm). The smallest species is likely *Paragonostomum minuta* (about 33 × 12 µm in protargol preparations). The ratio of body length to body width ranges from about 2–3:1 (e.g., *Kahliella*, *Parakahliella*, *Pseudokahliella*; e.g., Fig. 65a, 110a) to about 15–17:1 in *Circinella* in protargol preparations (e.g., Fig. 57o), that is, in life such slender species have a ratio of up to 20:1. Thus, the body outline ranges from elliptical to worm-like. The ventral side of most species is, as in the vast majority of the hypotrichs, flat, the dorsal side more or less distinctly vaulted; however, some have an almost circular cross-section (e.g., Fig. 86i, 90a). The body is flexible (supple) and usually acontractile or only slightly contractile. No species with a truly rigid body is described. In the Hypotricha, a rigid cortex/body is only known from the Stylonychinae, a subgroup of the oxytrichids (for review, see Berger 1999, p. 499), and some species of uncertain phylogenetic position, for ex-

[1] For names of higher taxa used in this book, see Fig. 6a, 9a and Table 3 in volume 3 (Berger 2008).

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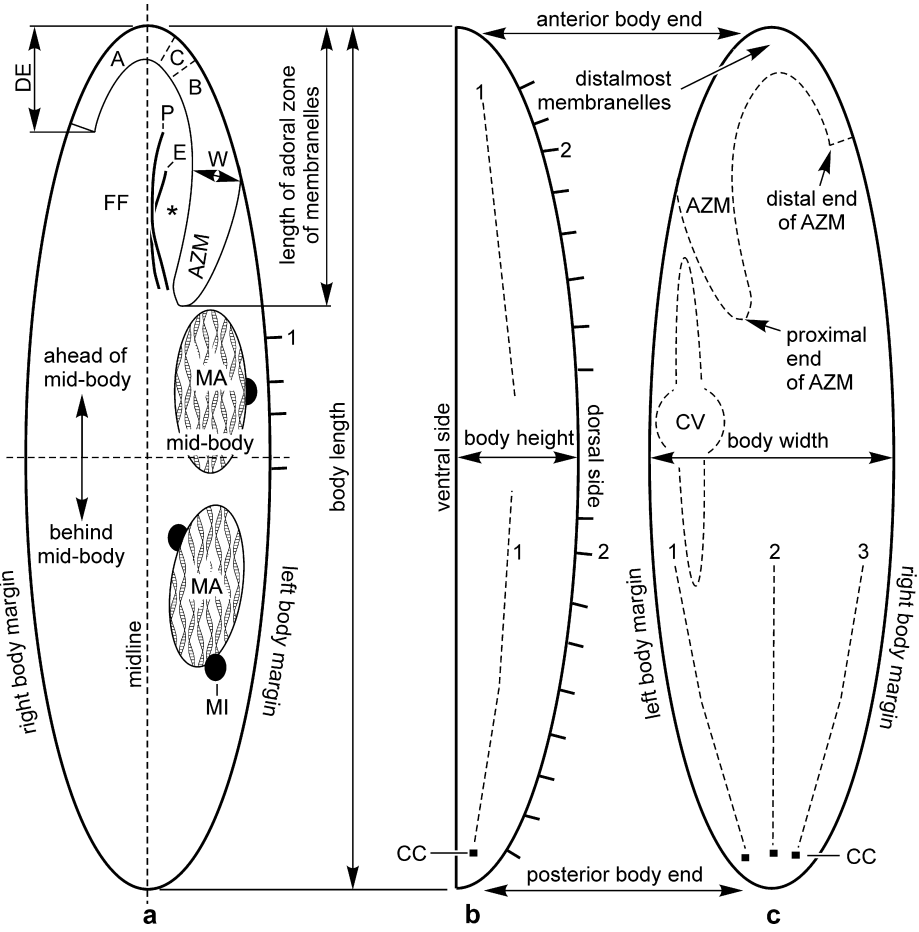


Fig. 1a–c Schematic illustrations to explain some general terms used in the species descriptions (from Berger 2008). **a:** Ventral view. Asterisk marks buccal cavity/field. **b:** Left lateral view. **c:** Dorsal view. A = distal (= frontal = collar) portion of adoral zone of membranelles, AZM = adoral zone of membranelles, B = proximal (= ventral = lapel) portion of adoral zone of membranelles, C = gap in adoral zone of membranelles (present in only some taxa), CC = caudal cirri, CV = contractile vacuole with collecting canals, DE = distance between anterior body end and distal end of adoral zone, E = endoral, FF = frontal field (area right of undulating membranes extending posteriorly to level of buccal vertex), MA = macronuclear nodule, MI = micronucleus, P = paroral, W = width of (largest) adoral membranelles, 1, 2, 3 = dorsal kineties with bristles (1 = leftmost kinety; kineties not shown in full length in [a, c]).

ample, *Rigidothrix* Foissner & Stoeck, 2006a or *Urospinula* Corliss, 1960 (Foissner 1983). The adoral zone of membranelles, the most prominent part of the oral apparatus, is in the left anterior body portion and usually occupies about 30–35% of body length, in some gonostomatids up to 50%. For some general terms used in the descriptions, see Fig. 1a–c.

1.2 Nuclear Apparatus

The species reviewed in the present book have an ordinary nuclear apparatus, that is, two or several macronuclear nodules and one or more micronuclei (Fig. 1a, Table 1). *Circinella* species have many (up to about 100) small macronuclear nodules (e.g., Fig. 57q) and for few species a single macronucleus is described (Table 1). Usually, the nuclear apparatus is somewhat left of or in body midline (e.g., Fig. 1a, 3a, 4b). As in other ciliate species, the nuclear pattern is very important for species identification. It is usually easily recognisable in life with differential interference microscopy, after staining with methyl-green pyronin, or after protargol impregnation (e.g., Fig. 24b).

The macronucleus is – as in most other ciliates – homomerous and polyploid. Homomerous means that there is no distinct differentiation into DNA-rich and DNA-poor parts, as is the case in the heteromerous macronuclei characterising groups like the Chlamydodontidae and Dysteriidae (Raikov 1969). For detailed reviews on the nuclear apparatus of hypotrichs and ciliates in general, see Raikov (1969, 1982, 1996), Klobutcher & Prescott (1986), Hoffman et al. (1995), Prescott (1994, 1998), and Bleyman (1996).

The development of the gonostomatid and kahliellid nuclear apparatus during cell division is the same as in many other hypotrichs. The micronuclei divide mitotically, whereas the fused macronucleus makes one or more rapid, successive amitotic divisions to produce the species-specific number of nodules in each filial product (Prescott 1994). Of course, the macronuclear nodules of the hypotrichs treated posses a replication band, a feature which evolved in the stem-line of the spirotrichs (e.g., Adl et al. 2005, Lynn 2008); for details on this feature see Olins & Olins (1994). For documentation of the division of the nuclear apparatus in gonostomatids and kahliellids, see, for example, *Gonostomum algicola* (Fig. 18c, p, 19b, h, j, l, n, p, r, t), *Kahliella simplex* (Fig. 67i–r, t–z, 68a–e, 70c, f, j), or *Engelmanniella mobilis* (Fig. 89c, g, i, j, l–n, q).

1.3 Contractile Vacuole and Cytopyge

The contractile vacuole is involved in osmoregulation to prevent a disruption of the cell due to the continuous influx of water into the ciliate. The influx occurs according to the osmotic gradient between the cytoplasm and the surrounding medium (Paulin 1996). The contractile vacuole of the taxa treated in the current volume is, as is usual for the hypotrichs, near the left cell margin at about 40–50% of body length or somewhat ahead of it; usually it is not ahead of the level of the proximal end of the adoral zone of membranelles (Fig. 1c, 2b). In some species (e.g., *Paragonostomum* spp., *Wallackia* spp.) it is somewhat displaced inwards (e.g., Fig. 33a, b, 104c), and in *Stenotricha arenicola* it is at about 60% of body length, that is, distinctly behind mid-body (Fig. 111b). Several species have more or less distinct col-

Table 1 Nuclear apparatus of gonostomatid and kahliellid ciliates and other species reviewed in this monograph

Nuclear apparatus	Species [a]
One macronucleus	*Cladotricha koltzowii* (Fig. 43a); *Orthoamphisiella breviseries* (Fig. 107a, e, g, i, j); *Strongylidium packii* (Fig. 50a)
Two macronuclear nodules; two or more micronuclei or number of micronuclei not known	*Afrokahliella binucleata* (Fig. 79a, f, h, i); *Afrokahliella namibicola*[b] (Fig. 76a, i); *Apourosomoida kahli* (Fig. 113a); *Apourosomoida variabilis* (Fig. 114h); *Cladotricha koltzowii* (Fig. 43j); *Cladotricha sagittata* (Fig. 44a); *Cladotricha sigmoidea* (Fig. 45a–c); *Cladotricha* sp. (Fig. 46a, b, 47a, b); *Deviata abbrevescens* (Fig. 96a, b, h); *Deviata bacilliformis* (Fig. 98b); *Deviata estevesi* (Fig. 104b, h); *Gonostomum affine* (Fig. 10a, b); *Gonostomum algicola* (Fig. 17a, 18a); *Gonostomum gonostomoidum* (Fig. 25b); *Gonostomum namibiense* (Fig. 22a, e, g, i); *Gonostomum* sp. (Fig. 27a, c); *Gonostomum strenuum* (Fig. 23a, e); *Gonostomum terrestre* (Fig. 26a, b); *Kahliella acrobates* (Fig. 62c); *Kahliella simplex* (Fig. 65g); *Neogeneia costata* (Fig. 85a, b); *Neogeneia hortualis* (Fig. 84a, c); *Neowallackia petergofi* (Fig. 55b); *Orthoamphisiella grelli* (Fig. 106a); *Paragonostomum binucleatum* (Fig. 35a, e, g); *Paragonostomum caudatum* (Fig. 30a, h, j); *Paragonostomum rarisetum* (Fig. 32a); *Perisincirra kahli* (Fig. 81a); *Perisincirra longicirrata* (Fig. 83a, e); *Sauditrix terricola*[h] (Fig. 108a, g); *Strongylidium packii* (Fig. 50a); *Trachelochaeta bryophila* (Fig. 56a); *Urosoma macrostomum* (Fig. 28a); *Wallackia bujoreani* (Fig. 40a, d); *Wallackia elegans* (Fig. 42a, c); *Wallackia schiffmanni* (Fig. 39a)
Two macronuclear nodules and one micronucleus in between	*Apourosomoida elongata* (Fig. 112a); *Perisincirra paucicirrata* (Fig. 82d, f)
Four macronuclear nodules (in some species the nodules are arranged in pairs)	*Afrokahliella halophila*[c] (Fig. 77a, n, p, r, t); *Afrokahliella namibicola*; *Apourosomoida kahli*; *Apourosomoida variabilis* (Fig. 114a); *Cladotricha koltzowii* (Fig. 43k–m); *Deviata bacilliformis* (Fig. 98a, c, n); *Deviata brasiliensis* (Fig. 100b); *Deviata polycirrata* (Fig. 102a, c); *Deviata quadrinucleata* (Fig. 99a, b); *Deviata spirostoma* (Fig. 101b); *Fragmocirrus espeletiae*[d] (Fig. 80a, g); *Gonostomum albicarpathicum*[f] (Fig. 21a, c); *Orthoamphisiella stramenticola* (Fig. 105a, j); *Stenotricha arenicola*[i] (Fig. 111b, d)
Five to eight, usually eight macronuclear nodules	*Engelmanniella mobilis*[e] (Fig. 86d, 87e); *Paragonostomum minuta* (Fig. 38c); *Paragonostomum multinucleatum*[g] (Fig. 33a, d, f, i, j); *Parakahliella haideri* (Fig. 75a, e); *Parakahliella macrostoma* (Fig. 73g); *Parakahliella terricola* (Fig. 74b)
More than eight macronuclear nodules	*Circinella arenicola* (Fig. 57a, q); *Circinella filiformis* (Fig. 61a, h); *Circinella vettersi* (Fig. 60a, f); *Cladotricha australis* (Fig. 48a, h); *Cladotricha halophila* (Fig. 49a, c); *Deviata rositae* (Fig. 103a–c); *Engelmanniella mobilis*[e] (Fig. 86k); *Gonostomum kuehnelti* (Fig. 15c; Fig. 123a, f in Berger 1999); *Neowallackia franzi* (Fig. 52a, e); *Neowallackia ghangriai* (Fig. 54c); *Paragonostomum simplex* (Fig. 36a); *Parakahliella haideri* (Fig. 75h); *Parakahliella macrostoma* (Fig. 73e); *Pseudokahliella marina* (Fig. 109a, g, 110i)

[a] For details on the nuclear apparatus, see individual descriptions.

[b] The number of macronuclear nodules varies from one to four.

Table 1 Continued

[c] Number of macronuclear nodules rather variable. The average ranges from 3.8 to 6.2; the minimum is two, the maximum is eight (Table 23).

[d] Rarely up to six macronuclear nodules present.

[e] Number of macronuclear nodules rather variable. Usually about eight nodules are present, the range is from five to 26 (Tables 28, 29).

[f] The range is from three to six (Table 14).

[g] On average seven macronuclear nodules, the range is from four to 13 (Table 16).

[h] Rarely three or four macronuclear nodules present.

[i] Two pairs of macronuclear nodules with single micronucleus in between.

lecting canals extending near the left body margin during diastole (e.g., Fig. 1c, 18a, 75c). Species living in highly saline habitats (*Cladotricha*, *Apourosomoida*) often lack a contractile vacuole. However, it is known that in halophile species the vacuole – if present at all – contracts in rather long intervals so that one cannot exclude that this organelle has sometimes been overlooked or misinterpreted as food vacuole. The excretory pore is, as in the other hypotrichs, on the dorsal side above the contractile vacuole (Fig. 88c).

Little is known about the cytopyge of the species treated in the present volume. Usually this organelle is located in the posterior body portion near the left cell margin (Fig. 52c).

1.4 Cytoplasm, Cortex, and Colouring

The cytoplasm of the gonostomatids, the kahliellids, and the other species treated in the present book is more or less colourless and contains the ordinary inclusions, for example, greasily shining globules, rod- and/or Y-shaped cytoplasmic crystals, and food vacuoles. Some species have cortical granules (see chapter 1.5) while symbiotic algae are not described.

The cortex of the species reviewed here is supple, that is, the body is flexible when freely motile. Consequently, it is very unlikely that your specimen/population belongs to a species described in the present book if its body is rigid and moves like a board when freely swimming; if you find such a specimen/population you have to look at the stylonychines (Berger 1999, p. 499); only very view other hypotrichs, for example, *Rigidothrix goiseri*, have a rigid body (Foissner & Stoeck 2006a). The ultrastructure of *Engelmanniella mobilis*, a species (preliminary) classified in the kahliellids was studied by Wirnsberger-Aescht et al. (1989), that of *Kahliella simplex* by Fleury et al. (1985, 1985a). Both species have a single layer of longitudinal microtubules underneath the somatic pellicle. Likely for that reason these and other

non-rigid species have a more or less flexible cortex. For details, see p. 367, 502 and individual papers.

1.5 Cortical Granules

Cortical granules occur in about 23% of the species reviewed (Table 2). Their size, shape, colour, and arrangement are very important features, which cannot usually be recognised after protargol impregnation. Consequently, live observation is absolutely necessary for a reliable identification of a hypotrich (e.g., Stein 1859, Kahl 1932, Borror & Wicklow 1983, Berger & Foissner 1987a, Foissner et al. 2002a, b). Note

Table 2 Gonostomatidae, Kahliellidae, and other species with cortical granules.

Species [a]	Granules			
	Size (µm)	Shape	Colour [b]	Arrangement and remarks
Afrokahliella binucleata (Fig. 79d, k)	1.0–1.3	globular	colourless	arranged in closely spaced, longitudinal rows; with central dark dot
Engelmanniella mobilis (Fig. 87b)	0.5–1.0	globular	colourless to yellowish	arranged in about 17 longitudinal rows; very conspicuous at high magnification
Gonostomum affine (Fig. 119c in Berger 1999)	<1.0	globular	colourless	loosely arranged in indistinct longitudinal rows
Gonostomum algicola (Fig. 18m, n)	0.8 × 0.5	rod-shaped	colourless, stain red when MGP is added	loosely spaced in longitudinal rows
Gonostomum kuehnelti (Fig. 123c, d in Berger 1999)	1.0–1.5	rod-shaped	colourless, stain red when MGP is added	loosely arranged
Gonostomum namibiense (Fig. 22c, d)	1.0 × 0.3	rod-shaped	colourless, stain red when MGP is added	closely spaced
Gonostomum strenuum (Fig. 122b, c in Berger 1999)	1.0–1.2 × 0.6	ellipsoidal	colourless, stain red when MGP is added	arranged in loose rows, form distinct fringe
Kahliella simplex (Fig. 65e)	>1.0	globular	colourless	arranged in loose rows
Neowallackia ghangriai	?	?	colourless	scanty dispersed; in addition to the cortical granules, extrusomes (1.6–2.1 × 0.6–0.7 µm after protargol impregnation, dispersed throughout body) are present

Table 2 Continued

Species	Granules			
	Size (µm)	Shape	Colour [a]	Arrangement and remarks
Paragonostomum minuta	?	?	?	few and scattered
Paragonostomum simplex (Fig. 36c, 37e)	≤0.50 × 0.25	ellipsoidal	colourless, stain red when MGP is added	loosely to densely arranged; not present in type population
Parakahliella macrostoma (Fig. 73b)	1–2	cylindrical	yellowish	web-like arranged crystals
Pseudokahliella marina (Fig. 109c)	about 1	globular?	colourless	arranged along cirral rows and in longitudinal rows; spindle-shaped and about 5–7 µm long when ejected
Stenotricha arenicola (Fig. 111e)	?	elliptical	?	scales covering entire cell disappearing slowly in morbid specimens
Wallackia bujoreani (Fig. 40b, e)	about 1.5	ellipsoidal	colourless	irregularly arranged; impregnate with protargol
Wallackia schiffmanni (Fig. 39b)	?	rod-shaped (spindle-shaped)	?	form distinct seam

[a] Species are arranged alphabetically. Further details see individual descriptions.

[b] MGP = methyl-green pyronin.

that the "correct" colour can only been seen at well-adjusted bright-field illumination; the presence or absence of cortical granules should be checked with differential interference contrast and by staining with methyl-green pyronin. For details on the ultrastructure of the cortical granules of *Engelmanniella mobilis*, see p. 502 (Wirnsberger-Aescht et al. 1989).

1.6 Movement

The species reviewed are – like the vast majority of the hypotrichs – usually thigmotactic, that is, they adhere more or less strongly to the substrate whenever the opportunity arises. They creep on their flattened ventral side by means of the cirri. Usually, the specimens move to and fro more or less hastily. All species have a supple body which bends to varying degrees. Thus, when you see a rigid, freely motile hypotrich you can exclude that it is treated in the present volume. No exhaustive stud-

ies on the movement of gonostomatids or kahliellids exists. Tailed or slender species are sometimes attached to the substrate via a fine thread (Fig. 30g).

1.7 Somatic Ciliature and Ultrastructure

As is usual for hypotrichs, the somatic ciliature of the Gonostomatidae, Kahliellidae, and the other taxa reviewed in the present book consists of rows and localised groups of cirri on the flattened ventral side, and several rows of more or less widely spaced, usually short (2–5 µm), stiff cilia (bristles) on the vaulted dorsal side (Fig. 1b). Many species have three dorsal kineties, a feature of the ground pattern of the Hypotricha (Berger 2008, p. 28). Caudal cirri are, if present at all, part of the dorsal ciliature because formed at the end of bipolar kineties (Fig. 1c, 2b). A "cirral row" in hypotrichs is either a true row (all cirri originate from the same anlage; e g., marginal row), a pseudorow (cirri originate from different anlagen; e.g., transverse cirri), or a mixed row (two or more "true" rows form a row; mainly present in the amphisiellids; see p. 10 and Fig. 1d–f in Berger 2008 for detailed explanation).

The arrangement of cirri and dorsal kineties is very important for the systematics. Consequently, as in other groups of hypotrichs, an unambiguous terminology is needed to describe and understand the morphology of the taxa treated (Fig. 1a–c, 2a, b, 3a, 4a, b). The paragraphs below describe the individual cirri and cirral groups. Many cirri of the various higher taxa of the hypotrichs (e.g., Urostyloidea, Oxytrichidae, Amphisiellidae, Trachelostylidae, Kahliellidae, Gonostomatidae) can be homologised and therefore have, of course, the same designation in these taxa. A detailed discussion of the confusing terminology of some cirri is provided by Berger (1999, 2006a). As in the previous volumes (Berger 1999, 2006a, 2008), I use the well-established numbering system introduced by Wallengren (1900) to designate the individual cirri and/or cirral rows and the anlagen from which these cirri originate (Fig. 2a); however, note that this system was basically established to characterise the pattern of 18-cirri hypotrichs (Fig. 6a in Berger 1999). In the following, the cirral groups and structures are explained in the same sequence as they are usually treated in the individual species descriptions. More specific terms are explained at the individual descriptions of genera and species.

Frontal cirri (FC). These cirri are near the anterior end of the cell (e.g., Fig. 2a, 3a, 4a). All taxa discussed have – like the oxytrichids, amphisiellids, trachelostylids, and many urostyloids – three more or less distinctly enlarged frontal cirri which usually form a slightly oblique pseudorow. In some gonostomatids the left cirrus is usually somewhat displaced posteriad and somewhat larger than the other two frontal cirri (e.g., Fig. 3a, 18b, 21f). The frontal cirri are undoubtedly homologous in all groups. The left one (= cirrus I/1) is usually ahead of the paroral. It is formed (in most cases) from the same anlage (= anlage I) as the undulating membranes. The middle cirrus is homologous to cirrus II/3 of, for example, the 18-cirri hypotrichs (Berger 1999). It is produced, like the buccal cirrus, from anlage II. The right frontal

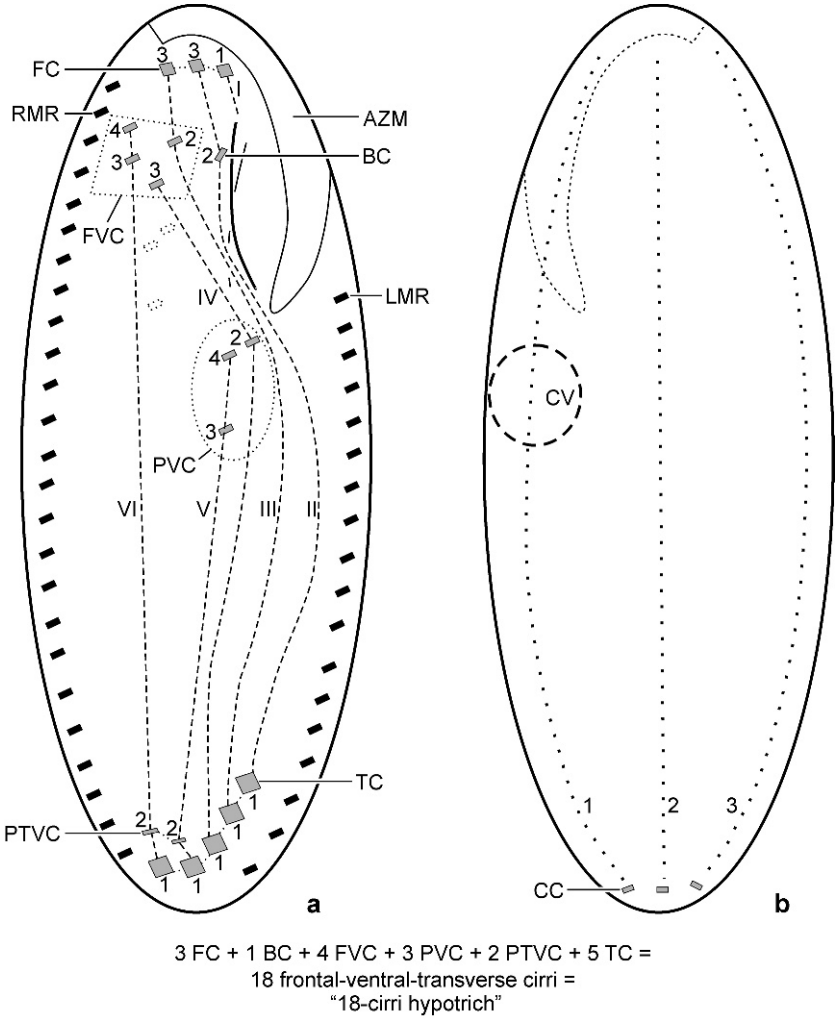


Fig. 2a, b Schematic illustration (from Berger 2008) of the ventral and dorsal side of the supposed last common ancestor of the Hypotricha (Fig. 6a, square 9 and Fig. 9a, square 1 in Berger 2008). The 18 frontal-ventral-transverse cirri and the three caudal cirri are grey, the marginal cirri are black. Broken lines connect cirri which originate from the same frontal-ventral-transverse cirri anlage; dotted lines in (a) connect or surround cirral groups. Perhaps the three postoral ventral cirri have been right of the proximal portion of the adoral zone in the last common ancestor (dotted cirri). The dorsal kinety pattern of the ancestor was very likely rather simplex, that is, composed of three bipolar kineties each bearing a caudal cirrus. Detailed explanation of structures, see text; details about the phylogeny, see chapter 2 in Berger (2008). AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri, CV = contractile vacuole, FC = frontal cirri, FVC = frontoventral cirri, LMR = left marginal row, PTVC = pretransverse ventral cirri, PVC = postoral ventral cirri, RMR = right marginal row, TC = transverse cirri, I–VI = frontal-ventral-transverse cirri anlagen, 1–4 = cirri within anlage (a), 1–3 = dorsal kineties (b).

cirrus (= cirrus III/3) is usually behind/close to the distal end of the adoral zone of membranelles.

Buccal cirrus (BC). This cirrus (= cirrus II/2) is usually right of the paroral (Fig. 2a, 3a, 4a); in some species it is ahead of the undulating membranes. For a discussion of the confusing terminology, see Berger & Foissner (1997) and Berger (1999). Most species reviewed in the present volume have one buccal cirrus which is certainly the plesiomorphic state. Few species, for example, *Neowallackia franzi* (Fig. 53a), *Saudithrix terricola* (Fig. 108f), or *Pseudokahliella marina* (Fig. 109f) have two or more buccal cirri. Usually, the buccal cirrus has an ordinary size, like, for example, the marginal cirri.

Parabuccal cirrus/cirri (PC; cirrus III/2). Usually, at least one parabuccal cirrus is present in the species treated in the current volume. Parabuccal cirrus is another designation for cirrus III/2, which is the cirrus behind the right frontal cirrus (Fig. 2a, 3a). In the 18-cirri hypotrichs, cirrus III/2 forms – together with cirri IV/3, VI/3, and VI/4 – the four frontoventral cirri (Fig. 2a, 36k; Fig. 6a in Berger 1999).

Frontoventral cirri (FVC). In 18-cirri hypotrichs (e.g., some *Gonostomum* species, Fig. 2a, 3a, 22e; Berger 1999) this group comprises four cirri (III/2, IV/3, VI/3, VI/4) between the anterior portion of the right marginal row and the paroral. They are arranged in various patterns, usually, however, in a V-shaped one (Berger 1999). Another term for the frontoventral cirri VI/3 and VI/4 is frontoterminal cirri (see next entry). When the number of cirri formed from the relevant anlagen is distinctly higher than one or two, then the species have frontoventral rows (see below).

Frontoterminal cirri (FT). This term was introduced by Hemberger (1982, p. 11) for the frontoventral cirri VI/3 and VI/4 (see previous entry) because they migrate to near the anterior body end in the middle and late phase of cell division (e.g., Fig. 36k). Borror & Wicklow (1983) thus designated these cirri, which never form primordia during morphogenesis, migratory cirri. In most species reviewed here not two, but more frontoterminal cirri are present, provided that anlage VI is available at all (Fig. 2a).

Frontoventral row. This is a general term for a cirral row formed from a frontal-ventral-transverse cirri anlage, usually anlage III (= parabuccal row), IV, V, or VI (Fig. 4a). Sometimes it is difficult to decide whether a row is a frontoventral row or a right marginal row. A relatively high number of species reviewed in the present volume lacks one anlage, respectively, the resulting frontoventral row. The genera and species treated have a rather different cirral pattern preventing a uniform designation of the individual structures, as, for example, in the 18-cirri hypotrichs. Nonetheless, I tried to apply a uniform terminology, as far as possible.

Postoral ventral cirri (PVC). In most 18-cirri hypotrichs this term is commonly used for the cirri IV/2, V/3, and V/4, which are behind the proximal end of the adoral zone (Fig. 2a). In *Gonostomum* species and some other taxa (trachelostylids, some *Lamtostyla*-species; Berger 2008), the postoral ventral cirri are displaced anteriad right of the proximal portion of the adoral zone of membranelles (e.g., Fig. 3a). Perhaps this is the older state within the hypotrichs (Berger 2008, p. 48).

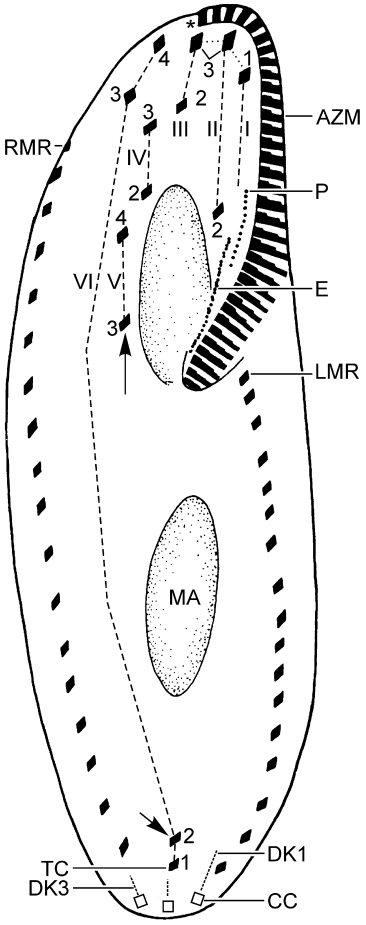


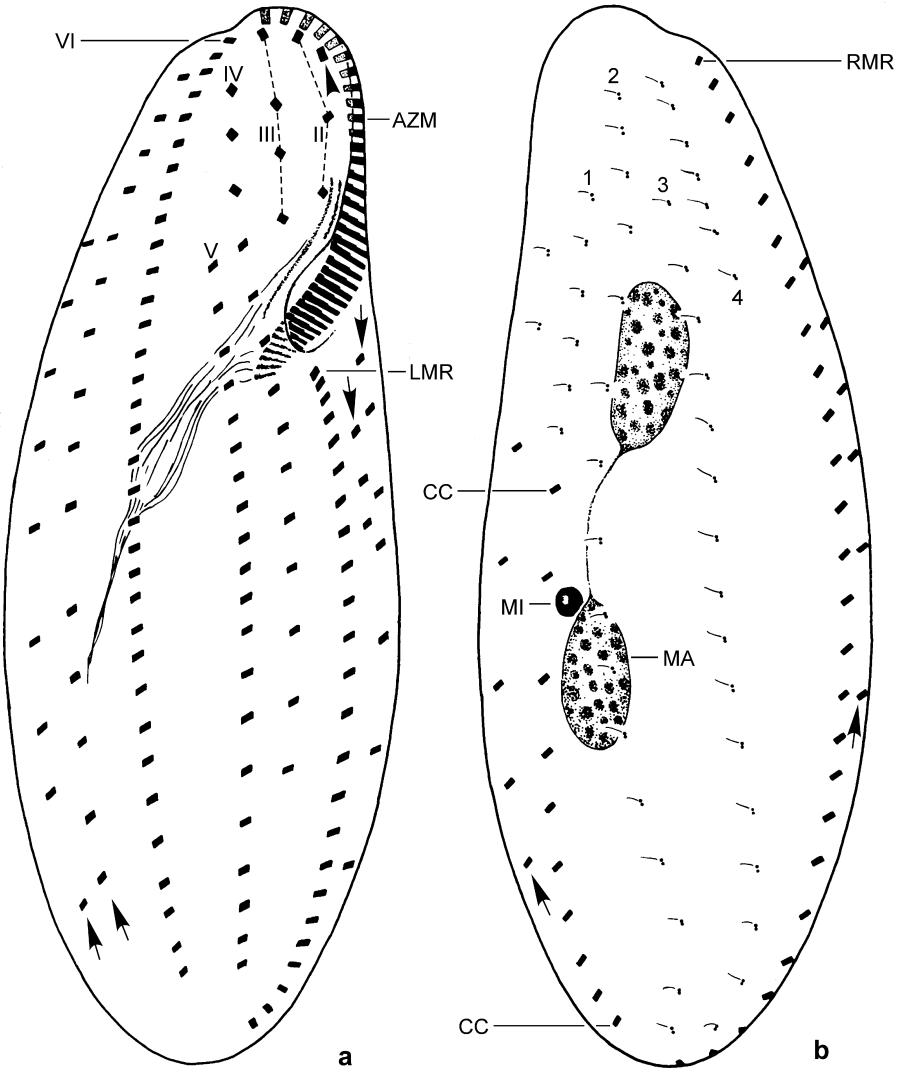
Fig. 3a *Gonostomum affine* (from Berger & Foissner 1988, slightly modified. Protargol impregnation). Infraciliature and macronuclear apparatus to show the general organisation of the gonostomatids. The most important features of this group are (i) the laterally extending and posteriorly knee-shaped adoral zone; (ii) the relatively few and rather widely spaced cilia/basal bodies forming the paroral; and (iii) the anteriorly displaced "postoral" ventral cirri (long arrow marks rearmost cirrus of this group). The short arrow denotes the pretransverse ventral cirrus originating from anlage VI. Note that *G. affine* is basically an 18-cirri hypotrich with a more or less distinctly reduced number of transverse cirri (cirri II/1, III/1, IV/1, V/1, V/2 [left pretransverse ventral cirrus] lacking in present specimen). Cirri III/2 (= parabuccal cirrus), IV/3 (anteriormost cirrus of anlage IV), and VI/3, and VI/4 (frontoterminal cirri) form the frontoventral cirri. Broken lines connect cirri originating from the same anlage (I–VI); dotted line connects frontal cirri. AZM = adoral zone of membranelles, CC = caudal cirri (usually on dorsal side), DK1, 3 = dorsal kineties (arranged on dorsal side and therefore only the rear portion is schematically shown; kinety 2 not labelled), E = endoral, LMR = left marginal row, MA = macronuclear nodule, P = paroral, RMR = right marginal row, TC = transverse cirrus/cirri, I–VI = frontal-ventral-transverse cirri anlagen, 1–4 = numbering of cirri within anlagen I–VI (numbered from posterior to anterior according to system by Wallengren 1900). Description of species, see page 68.

Pretransverse ventral cirri (PTVC; PT in Berger 2006a). This term was introduced by Berger & Foissner (1997) for two cirri of 18-cirri hypotrichs (Fig. 2a). Accessory transverse cirri is an older, synonymous term introduced by Wicklow (1981, p. 348). They are usually arranged immediately ahead of the transverse cirri V/1 and VI/1 and are designated V/2 and VI/2 according to Wallengren's scheme. The present volume treats only a limited number of species having pretransverse ventral cirri, for example *Gonostomum namibiense* (e.g., Fig. 22e). In species with a reduced number of pretransverse ventral and transverse cirri they are often difficult to distinguish because it is not known which cirri have been lost; in addition, the size of cirri of these two groups is often rather similar. In such cases, ontogenetic data are needed for a correct designation.

Transverse cirri (TC). These cirri, which often form a distinct pseudorow, are usually in the posterior quarter of the cell (e.g., Fig. 2a, 3a, 15a, 108f). Transverse cirri are part of the ground pattern of the Hypotricha (Berger 2008, p. 35) and therefore present in many hypotrichs. However, in most kahliellids and many gonosto-

matids they are rather inconspicuous or even lacking (Fig. 3a, 4b). Further details, see Berger (2008, p. 16).

18-cirri hypotrich. The last common ancestor of the Hypotricha very likely had 18 frontal-ventral-transverse cirri arranged in a highly characteristic pattern originating from six (I–VI) anlagen (e.g., Fig. 2a; Fig. 6a in Berger 1999). Consequently, this pattern occurs at just about all sites of the Hypotricha tree. Previously I thought that this curious cirral pattern is an apomorphy of the oxytrichids (Berger & Foissner 1997, Berger 1999). By contrast, Eigner (1997, p. 553) and some other workers supposed that the 18 cirri have evolved several times independently. However, this is



almost impossible because the pattern, including its formation, is too complex to evolve convergently. Further details, see Berger (2008, p. 23).

Marginal cirri (LMR, RMR). These cirri run along the left and right body margin. Most hypotrichs have one left and one right marginal row (Fig. 2a, 3a, 4a, b). Marginal rows are true cirral rows because all cirri of each row originate from the same anlage. The right marginal row often commences near the distal end of the adoral zone; in some species it is distinctly shortened anteriorly or it extends onto the dorsolateral surface. The left row usually begins left of the proximal portion of the adoral zone. In most species the marginal rows are slightly shortened posteriorly, that is, they do not extend to the posterior tip of the cell so that the rows are distinctly separated. However, the gap between the rows is sometimes difficult to recognise because it is seemingly occupied by the caudal cirri, which, however, insert on the dorsal side. A rather high number of species reviewed in the present book has more than two marginal rows, for example, *Kahliella* spp. (Fig. 4a, b), *Deviata* (Fig. 96g), *Fragmocirrus* (Fig. 80f), *Saudithrix* (Fig. 108f, h), or *Pseudokahliella* (Fig. 109f). However, sometimes it is difficult to distinguish between frontoventral row and right marginal row. In some species the additional marginal rows are new rows, that is, they originate from a primordium (e.g., *Saudithrix*). In most species with more than two marginal rows, the additional rows are remnants of the parental or grand-parental generation (e.g., *Kahliella* spp., *Engelmanniella*). This feature – its formation was termed neokinetal wave by Eigner (1995, p. 343) – is also known from other groups, for example, the stylonychine *Coniculostomum* (Kamra & Sapra 1990; for review, see Berger 1999, p. 606), showing that this relatively simple feature evolved convergently.

Dorsal cilia (DB; 1, 2, 3, ...). The dorsal side of all hypotrichs and euplotids is covered by a more or less high number of kineties, which are therefore named dorsal kineties or dorsal bristle rows (e.g., Fig. 1a–c, 2b). The gonostomatids have – like many urostyloids and amphisiellids – three bipolar kineties (Fig. 2b, 10j, 18c), which is likely the state in the stem line of the hypotrichs (Berger 2008, p. 28). Previously, that is, when I assigned *Gonostomum* to the Oxytrichidae (Berger 1999, p. 367), I hypothesised that this simple pattern (dorsomarginal kineties and fragmentation lacking) evolved from the *Oxytricha*-pattern (dorsomarginal kineties and kinety fragmentation present) via the *Urosomoida*-pattern (loss of kinety fragmentation). The kineties of the Gonostomatidae are basically bipolar, that is, they extend from

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← **Fig. 4a, b** Infraciliature of ventral and dorsal side and nuclear apparatus of a typical kahliellid (*Kahliella simplex*; from Berger & Foissner 1987. Protargol impregnation). Arrowhead in (a) marks left frontal cirrus (= cirrus I/1). Arrows mark old cirral rows from previous generations with widely spaced cirri. The preservation of parental ciliature is the main (relatively weak) feature of the kahliellids (details see systematic section). The major differences to the gonostomatids (Fig. 3a, b) are the presence of a dorsomarginal kinety (kinety 4 in b) and the preservation of parental cirri. AZM = adoral zone of membranelles, CC = caudal cirri (= rear portion of dorsal kinety 1), LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row, I–VI = frontoventral cirri rows (= cirri originating from anlagen I–VI), 1–4 = dorsal kineties. Description of species, see page 367.

near the anterior to near the posterior body end. Dorsomarginal kineties, which originate from/near the right marginal primordium, are present in the Kahliellidae, although this feature is not yet confirmed for the type species of *Kahliella*. Fragmenting kineties are lacking in all taxa reviewed in the present book. Fragmentation is characteristic for the oxytrichids[1] (for review, see Berger 1999; 2006a, p. 1190) and few other taxa (e.g., *Trachelostyla pediculiformis*; Berger 2008, p. 478), whereas dorsomarginal kineties are probably the main morphological apomorphy of the Dorsomarginalia (Berger 2006a). The importance of the dorsal kinety pattern in elucidating the phylogeny of the hypotrichs has been underestimated for a long time (Foissner & Adam 1983a). Recent molecular studies largely support groups based on features of the dorsal kinety pattern. Its exact description is therefore an absolute prerequisite for a serious description and classification of a hypotrich.[2] However, ontogenetic data are often needed to understand a pattern correctly, that is, to know whether or not dorsomarginal rows and/or kinety fragmentation are present.

Caudal cirri (CC). They originate at the posterior end of the bipolar dorsal kineties, that is, they are part of the dorsal infraciliature (Fig. 1c, 2b). Dorsomarginal kineties, present in most kahliellids but lacking in all other species reviewed in the present volume, are never associated with caudal cirri, that is, in the latter group (non-kahliellids) the number of caudal cirri (if present at all) is usually equal to the number of dorsal kineties, assuming that each kinety forms one cirrus. In *Parakahliella* and *Afrokahliella* only kineties 1 and 2 produce caudal cirri, sometimes however, up to 12 per row (Table 23). The caudal cirri are arranged dorsally, usually at or very close to the rear body end, frequently above the gap formed by the rear end of the marginal rows. Thus, live and silver preparations must be studied with high diligence to avoid a misinterpretation of caudal cirri as marginal or transverse cirri or vice versa. In vermiform species it is sometimes impossible to decide whether cirri at the rear cell end are caudal, transverse, or marginal cirri, even in protargol preparations. In such cases, ontogenetic data are indispensable for a correct interpretation. The caudal cirri of many species are rather inconspicuous, that is, neither very long and/or strong. In *Wallackia*, however, they are very prominent because they are long and look like Pasteur pipettes (Fig. 39a, d, 42l). The presence of caudal cirri is a plesiomorphy in the reviewed taxa because they are (very likely) already part of the ground pattern of the hypotrichs (Berger 2008, p. 35). Some taxa lack caudal cirri (e.g., *Engelmanniella*, *Neowallackia*). There is no doubt that the loss, a rather simple feature, occurred many times independently in the hypotrichs (Berger 1999, 2006a, 2008).

Fine structure of cirri and membranelles. Studies about this topic are rare. Fleury et al. (1985) investigated a *Kahliella* species whereas Wirnsberger-Aescht et

[1] Note that the fragmentation present in *Apourosomoida halophila* (Fig. 110q in Berger 2008) is very likely not homologous to the oxytrichid fragmentation.

[2] For the determination of a hypotrich it is, however, often not necessary to know the dorsal kinety pattern exactly.

al. (1989) analysed the ultrastructure of *Engelmanniella mobilis*. For some details see the systematic section and the individual papers.

1.8 Oral Apparatus

The oral apparatus is composed, as in the other hypotrichs, of an adoral zone of membranelles, two undulating membranes (paroral and endoral), the buccal cavity (buccal field, oral field), and associated fibres including the cytopharynx. For a detailed characterisation and terminology of the various oral types present in the hypotrichs, see Berger & Foissner (1997), Berger (1999, 2006a, 2008), and Foissner & AL-Rasheid (2006). Detailed studies of the oral apparatus will provide further interesting differences among various taxa. However, these features are generally very sophisticated and at present known only for a very low number of species.

The adoral zone of membranelles extends from the anterior body end roughly along the left body margin to near midline of the cell and usually terminates at about 20–35% of body length. In some taxa, for example, *Circinella* and *Engelmanniella*, the adoral zone occupies only 6–16% of body length while it is very large (sometimes up to 50%) in *Pseudokahliella* and some gonostomatids (e.g., Fig. 24a–d). In most hypotrichs it is more or less shaped like a question mark and the distal end does not extend far posteriorly, that is, the so-called DE-value[1] is often less than 0.11 (Berger 2006a, p. 18). In the gonostomatids and in *Kahliella* the shape of the zone is rather characteristic because the middle range extends along the left body margin while the proximal part bends knee-shaped towards the cell-midline (Fig. 3a, 4a). In addition, the relative length of the zone is often near 50% of body length, a value also known from the stylonychines (Berger & Foissner 1997, Berger 1999).

Apourosomoida species (p. 684) and other hypotrichs have a more or less distinct gap (break) in the adoral zone at the left anterior body corner (e.g., Fig. 114g; further examples see Berger 2006a, 2008). The anterior, often transversely arranged portion is termed distal, frontal, or collar portion and largely on the dorsal side of the frontal scutum, the anteriormost part of the body; the posterior part of the zone is termed proximal, ventral, or lapel portion. The membranelles of the species treated in the present volume very likely have the ordinary fine structure, that is, each membranelle is composed of (i) two long kineties, (ii) one moderately long kinety, and (iii) one short kinety. For details on the ultrastructure in *Kahliella simplex* (p. 367) and *Engelmanniella mobilis* (p. 502), see Fleury et al. (1985) and Wirnsberger-Aescht et al. (1989).

Hypotrichs have two undulating membranes, the paroral and the endoral[2] (e.g., Fig. 3a, 78a, 108m). For detailed discussion of various patterns formed by the mem-

[1] DE-value = distance DE divided by length of adoral zone of membranelles (Fig. 1a; Berger 2006a, 2008).

[2] Note that the paroral and the endoral have been confounded sometimes (e.g., Wirnsberger-Aescht et al. 1989).

branes, including the *Gonostomum*-pattern (e.g., Fig. 3a, 24b–d), see Berger & Foissner (1997) and Berger (1999). In general, the paroral extends between two, usually inconspicuous cytoplasmic lips at the right outer margin of the buccal cavity, that is, on the cell surface, while the endoral is on the bottom and right wall of the cavity (Foissner & AL-Rasheid 2006). This means that the membranes are at different levels, but when the cell is viewed from the ventral side, they appear to lie side by side or to intersect, depending on their shape and arrangement. The buccal cavity is covered by a very fine membrane, the so-called phago-assistant membrane (Sui et al. 2001) or buccal seal (Foissner & AL-Rasheid 2006). The buccal cavity is of different size and shape, usually described by the terms flat or deep and wide or narrow. Flat means that the cavity is only slightly hollowed, whereas a deep cavity extends to near the dorsal side of the cell, making the field conspicuously bright. In species with a wide cavity (e.g., *Saudithrix*; Fig. 108a, t), the right margin of the cavity is in the midline of the cell, whereas in a narrow cavity (e.g., gonostomatids) it is close to the right margin of the adoral zone (further details, see Berger & Foissner 1997, Berger 1999, Foissner & AL-Rasheid 2006).

1.9 Silverline System

The silverline system of the hypotrichs is composed of small (1–2 µm), polygonal meshes (Fig. 39c, 109b). It has no systematic value in the hypotrichs, although it is successfully used to characterise euplotids (e.g., Curds & Wu 1983, Foissner et al. 1991, Borror & Hill 1995) and other ciliate taxa (e.g., Foissner 1993, Foissner et al. 1995).

1.10 Life Cycle

The species reviewed in the present book have, like most other hypotrichs, (very likely) a normal life cycle, that is, the specimens feed, become well nourished[1] and divide, encyst, or conjugate (e.g., Foissner & Xu 2007).

1.10.1 Cell Division

The species treated in the current volume breed by isotomic transverse fission, like many other ciliates (for review, see Foissner 1996). For a detailed description of a cell division, see *Gonostomum affine* (Fig. 11b–m; Eigner 1999), *G. kuehnelti* (Fig. 16a–j; Eigner 1999), *G. algicola* (Fig. 18o–s, 19a–t; Foissner et al. 2002a), *Wallackia bujoreani* (Fig. 41a–p; Foissner et al. 2002a), *Cladotricha halophila* (Fig. 49e–s; Wilbert 1995), *Neowallackia franzi* (Fig. 53a–w; Berger & Foissner 1988), *Circinella ar-*

[1] For comments on the terms trophont and theront, see last paragraph of the remarks at *Circinella* (p. 314).

enicola (Fig. 59a–q; Foissner 1994a), *Kahliella simplex* (Fig. 70a–o; Fleury & Fryd-Versavel 1982, Eigner 1995), *Parakahliella macrostoma* (Fig. 73h–q; Berger et al. 1985), *P. haideri* (Fig. 75k–w; Berger & Foissner 1989b), *Fragmocirrus espeletiae* (Fig. 80h; Foissner 2000), *Neogeneia hortualis* (Fig. 84d–n; Eigner 1995), *Engelmanniella mobilis* (Fig. 89a–q; Wirnsberger-Aescht et al. 1989), *Deviata abbrevescens* (Fig. 96j–p; Eigner 1995), and *Orthoamphisiella stramenticola* (Fig. 105j–t; Eigner & Foissner 1993). Further ontogenetic data of *Gonostomum* and *Apourosomoida* are reviewed by Berger (1999, 2008).

The anterior filial product is the proter, the posterior the opisthe. During very early phases of division, a replication (= reorganisation) band traverses each macronuclear nodule (Olins & Olins 1994), a feature already occurring near the base of the spirotrichs (Lynn 2008, p. 347). The two to several nodules fuse to a single mass in early and middle dividers. By contrast, the micronuclei divide mitotically (details on nuclear apparatus, see chapter 1.2).

The principles of the formation of the frontal-ventral-transverse cirri in the species reviewed in the current volume are basically as in many oxytrichids (Berger 1999) and amphisiellids (Berger 2008), simply because (i) all groups evolved from a hypotrich which very likely produced 18 cirri from six (I–VI) anlagen and (ii) most species reviewed here still have five or six anlagen. Consequently, many plesiomorphic features occur in all these taxa, for example, the formation of the left frontal cirrus from anlage I, the formation of the middle frontal cirrus and the buccal cirrus/cirri from anlage II, or the migration of the frontoterminal cirri (if present at all). Of course, there are distinct deviations between the genera and species treated because they have rather different cirral patterns. Thus, the reader is referred to the individual genera where morphogenetic similarities with other taxa are discussed. Eigner (1995, 1997, 1999) concentrated rather strongly on few ontogenetic features resulting in a complex classification which is largely not supported by other morphologic and ontogenetic data and molecular analyses. The cirral and dorsal kinety pattern of the species reviewed here are rather divers and since I am not totally convinced that the groups treated (especially the kahliellids) are monophyletic I do not provide a comprehensive morphogenetic review. For details on the individual genera and species, see systematic section.

The new marginal rows are usually formed within the parental marginal rows, that is, two anlagen are produced within each row, one at the anterior end and one roughly in mid-body. Generally, the anlagen for the dorsal kineties occur at about the same level as the anlagen for the marginal rows indicating these structures are homonomous (e.g., Fig. 73m, n; Berger et al. 1985). In several taxa (e.g., *Kahliella*, *Engelmanniella*, *Neogeneia*) marginal rows of the previous generations are retained resulting in rather complex cirral patterns; preliminary this is considered as main feature of the kahliellids (Fig. 4a, b).

Usually, dorsal morphogenesis proceeds rather simple when only three or more bipolar kineties are present as, for example, in the gonostomatids. Briefly, two anlagen occur within each parental kinety (e.g., Fig. 19j, l); dorsomarginal kineties and

an oxytrichid kinety fragmentation do not occur. The same pattern is known from the urostyloids (Berger 2006a) and the amphisiellids (Berger 2008). *Kahliella simplex* has bipolar kineties and a dorsomarginal row (Fig. 65g, 70h, k), showing that the kahliellids are a member of the Dorsomarginalia, but not of the oxytrichids. Preliminary molecular data, however, do not support this hypothesis (details see remarks at the Kahliellidae). *Apourosomoida halophila*, type of *Apourosomoida* Foissner et al., 2002, shows a dorsal kinety fragmentation which is, however, (very likely) not homologous to that of the oxytrichids (for review, see Berger 2008). Some taxa have peculiarities in dorsal kinety formation. For example, parental kineties are retained in postdividers of *Parakahliella macrostoma* (Fig. 75r, u), and in *Engelmanniella mobilis* dorsal kinety 2 of the opisthe originates de novo, that is, without contact to parental ciliature (Fig. 89g).

Caudal cirri originate at the rear end of bipolar dorsal kineties (Fig. 2a, 19n, p), but not at the end of dorsomarginal rows. Three caudal cirri are perhaps an apomorphy of the Hypotricha (Berger 2008, p. 289), that is, within the Hypotricha the presence of three caudal cirri is a plesiomorphy. Several taxa have lost the caudal cirri, a rather simple feature which very likely evolved several times independently in the hypotrichs.

Kahliella species have dorsal rows composed of bristles and cirri about in equal share (e.g., Fig. 4b). Eigner (1995, p. 343) introduced the term “combined cirral row” for such a kinety. I designate it as dorsal kinety 1; however, basically this is only a terminological problem.

1.10.2 Conjugation

Conjugation is studied more or less detailed in *Kahliella simplex* (p. 367) and *Engelmanniella mobilis* (p. 502). The principles of this part of the life cycle are similar in all ciliates, so please refer to reviews dealing with other groups of hypotrichs (Berger 1999, 2006) or ciliates (e.g., Dini & Nyberg 1993, Miyake 1996, Xu & Foissner 2004, Foissner & Xu 2007, Vdacný & Foissner 2008).

1.10.3 Cyst

Little information about the dormant period of the life cycle is available. Only the resting cysts of *Kahliella simplex* (p. 367; Foissner I. & Foissner W. 1987) and *Engelmanniella mobilis* (p. 502; Wirnsberger-Aescht et al. 1990) have been investigated in detail (for reviews, see Gutiérrez et al. 2003, Foissner 2005). If data are available then they are mentioned in the description of the individual species. Reproductive cysts – characteristic for the keronopsids (*Keronopsis*, *Paraholosticha*; e.g., Dieckmann 1988, 1989) – are not known for taxa discussed here. According to Foissner et al. (2008, p. 349), the number of so-called cyst species (two or more spe-

cies which differ mainly in cyst morphology) is rather high. The ultrastructure of the resting cysts supports in several cases the phylogenetic hypotheses based on morphology and gene sequence data (see remarks at the Gonostomatidae).

1.10.4 Reorganisation, Regeneration, Doublets

Like other hypotrichs, the gonostomatids, kahliellids, and the other taxa reviewed in the present book produce ciliature not only during cell division, conjugation, and excystment, but also during physiological reorganisation. However, only very few data are available about this process. Generally, the formation of the ciliature proceeds very similar during reorganisation and cell division.

2 Phylogeny

In this chapter the phylogenetic position of the two major groups (Gonostomatidae and Kahliellidae) reviewed in the present book are briefly discussed. For details, see systematic section. Notes on the nomenclature of the Spirotricha Bütschli, 1889 and the Hypotricha Stein, 1859 can be found in Berger (2008, p. 23). Nomenclatural problems concerning the Gonostomatidae and the Kahliellidae are discussed in the systematic section. The ground pattern of the Hypotricha, that is, the combination of features (apomorphies and more or less young plesiomorphies) of the stem-species from which the monophylum evolved, is described and discussed in detail by Berger (2008, p. 23). The relationships within the spirotrichs and hypotrichs are hypothesised in Fig. 6a, 9a of Berger (2008). Unfortunately, the numerous molecular trees dealing with these groups differ from each other more or less distinctly, a problem usually not discussed in the individual papers. The inhomogeneity of the published phylogenies demonstrates that the results should not be overinterpreted.

Previously, *Gonostomum* – the name-bearing type of the Gonostomatidae – has been assigned to the Oxytrichidae because the type species (*G. affine*) has basically an 18-cirri pattern (Fig. 3a), a feature considered as apomorphy of the oxytrichids (Berger & Foissner 1997, Berger 1999). A new hypothesis about the evolution of the ventral and dorsal infraciliature and molecular data indicate that *Gonostomum* branches off rather early in the Hypotricha tree, namely outside the so-called Dorsomarginalia (Fig. 9a in Berger 2008); thus, the Gonostomatidae are reactivated. The simple dorsal kinety pattern (only bipolar kineties present) places the amphisiellids and the urostyloids in a very similar position within the Hypotricha tree (Berger 2006a, 2008), an assumption largely supported by gene sequence data. For a more detailed discussion of the phylogenetic position of the gonostomatids, see p. 51.

The Kahliellidae are, in contrast to the gonostomatids, a widely accepted taxon (Tables 5–13). Unfortunately, a strong, convincing apomorphy is lacking, indicating that this group is a non-monophyletic assemblage. The type species of the name-

bearing genus *Kahliella*, *K. acrobates*, is not yet described in detail. The very similar and perhaps synonymous *K. simplex* has a dorsomarginal row and bipolar kineties indicating that it is a non-oxytrichid dorsomarginalian (Fig. 9a in Berger 2008). At present, molecular data are scanty and lame and therefore should be interpreted with caution. A not yet described *Kahliella* species clusters within the oxytrichids. Further details, see p. 341, 347.

3 Previous Classifications and Revisions

3.1 General

The original classifications and some later schemes are presented in Tables 3–13. I did not change the original presentations, that is, (i) the sequence of the genera; (ii) the spelling of the genus and author(s) names; and (iii) the year of publication[1] are as in the publications. For brief discussion of the schemes shown in the tables, see the systematic section. Many species and genera – although classified by some authors in the gonostomatids or kahliellids – are not considered in the present monograph. For an explanation of the exclusion, see the chapters "Taxa not considered ..." (p. 339, 545).

3.2 Gonostomatidae

The "family Gonostomatidae" was established by Small & Lynn (1985), together with the Cladotrichidae Small & Lynn, 1985 and the Trachelostylidae Small & Lynn, 1985. Later, the Gonostomatidae have been submerged in the Trachelostylidae, whereas the Cladotrichidae have been synonymised with the Kahliellidae (Lynn & Small 2002, Lynn 2008). In the review on the oxytrichids I put the gonostomatids into the synonymy of the Oxytrichidae because I regarded *Gonostomum* as an oxytrichid which had a simple dorsal kinety pattern due to a loss of both kinety 3 fragmentation and dorsomarginal kineties (Berger 1999). The assignment of *Gonostomum* to the oxytrichids was maintained by Jankowski (2007). Now I am convinced that this was incorrect and therefore reactivate the Gonostomatidae to include species and genera with have the characteristic gonostomatid oral apparatus and the simple dorsal kinety pattern taken over from the last common ancestor of the Hypotricha. Since *Cladotricha* also fits this combination of features I include it in the Gonostomatidae, that is, I synonymise the Cladotrichidae with the Gonostomatidae.

[1] Note that possibly not all "nomenclatural" references of Tables 3–13 are included in the reference section of the present book. For a "complete" bibliography of hypotrichs and euplotids, see Berger (2001, 2006b).

The trachelostylids are now a small group of marine 18-cirri hypotrichs (Berger 2008, p. 471).

Table 3 Classification of gonostomatid ciliates according to Small & Lynn (1985)

Family Gonostomatidae n. fam.
Trachelochaeta
Wallackia
Gonostomum

Table 4 Classification of cladotrichid ciliates according to Small & Lynn (1985)

Family Cladotrichidae n. fam.
Engelmanniella
Uroleptoides
Cladotricha
Lamtostyla
Perisincirra

3.3 Kahliellidae

The "family Kahliellidae" was established by Tuffrau (1979), a group not accepted by Hemberger (1982), Small & Lynn (1985), and Eigner (1997, 1999). They classified *Kahliella*, type of the group, in the Amphisiellidae (Hemberger 1982, Small & Lynn 1985) or Oxytrichidae (Eigner 1997, 1999). Eigner (1997) introduced the Parakahliellidae comprising *Parakahliella macrostoma* as type, but also many oxytrichids. Later, this group was submerged in the kahliellids (Lynn & Small 2002, Jankowski 2007, Lynn 2008).

There exists no modern, detailed revision of the Kahliellidae. The review by Kahl (1932) contains only very few species because most kahliellids are soil inhabitants most of which have been discovered just in the last decades. Consequently, many species of this taxon have been described more or less detailed after silver impregnation. Unfortunately, the Kahliellidae are not well defined because a strong morphological and/or ontogenetic apomorphy is lacking. Thus, they are rather a melting pot for species and genera with a more or less high number of cirral rows than a monophyletic group. Molecular data are sparse and also do not support the classifications previously proposed for the kahliellids.

Table 5 Classification of kahliellid ciliates according to Tuffrau (1979)

Famille Kahliellidae n. fam.
Uroleptus Ehrenberg, 1831
Psilotricha Stein, 1859
Eschaneustyla Stokes, 1886
Hemicycliostyla Stokes, 1886
Cladotricha Gajewskaja, 1926

Table 5 Continued

Paraholosticha Kahl, 1932
Uroleptopsis Kahl, 1932
Uncinata Bullington, 1940
Uroleptoides Wenzel, 1953
Kahliella Corliss, 1960
Spirofilopsis Corliss, 1960
Urospinula Corliss, 1960

Table 6 Classification of kahliellid ciliates according to Tuffrau (1987)

Famille Kahliellidae Tuffrau, 1979
Cladotricha Gajewskaja, 1926
Engelmanniella Foissner, 1982
Eschaneustyla Stokes, 1886
Hemicycliostyla Stokes, 1886
Kahliella Corliss, 1960
Paragastrostyla Hemberger, 1981
Paraholosticha Kahl, 1932
Parakahliella Berger, Foissner et Adam, 1985
Periholosticha Hemberger, 1981
Perisincirra Jankowski, 1979
Pseudokahliella Berger, Foissner et Adam, 1985
Pseudouroleptus Hemberger, 1981
Psilotricha Stein, 1859
Spirofilopsis Corliss, 1960
Uncinata Bullington, 1940
Uroleptoides Wenzel, 1953
Uroleptopsis Kahl, 1932
Uroleptus Ehrenberg, 1831
Urospinula Corliss, 1960

Table 7 Classification of kahliellid ciliates according to Tuffrau & Fleury (1994)

Famille de Kahliellidae Tuffrau, 1979
Cladotricha Gajevskaja, 1925
Engelmanniella Foissner, 1982
Eschaneustyla Stokes, 1886
Hemicycliostyla Stokes, 1886
Kahliella Corliss, 1960
Paragastrostyla Hemberger, 1981
Paraholosticha Kahl, 1932
Parakahliella Berger et al., 1985
Pseudokahliella Berger et al., 1985
Pseudouroleptus Hemberger, 1981
Psilotricha Stein, 1859
Uncinata Bullington, 1940
Uroleptoides Wenzel, 1953
Uroleptus Ehrenberg, 1831
Urospinula Corliss, 1960

Table 8 Classification of kahliellid ciliates according to Eigner (1995)

Family Kahliellidae Tuffrau, 1979
Deviata nov. gen.
Neogeneia nov. gen.
Kahliella (Horváth, 1932) Corliss, 1960
Engelmanniella Foissner, 1982
Parakahliella Berger, Foissner and Adam, 1985
Coniculostomum (Dragesco and Njiné, 1971) Njiné, 1979
Paraurostyla weissei
Onychodromus quadricornutus
Laurentiella acuminata

Table 9 Classification of kahliellid ciliates according to Shi et al. (1999) and Shi (1999)

Kahliellidae Tuffrau, 1979
Engelmanniella Foissner, 1982
Kahliella Gorliss, 1960

Table 10 Classification of kahliellid ciliates according to Lynn & Small (2002)

Family Kahliellidae Tuffrau, 1979
Neogeneia Eigner, 1995
Pseudokahliella Berger, Foissner and Adam, 1985
Kahliella Corliss, 1960
Trachelochaeta Srámek-Husek, 1954
Wallackia Foissner, 1977
Paraurostyla Borror, 1972
Parakahliella Berger, Foissner and Adam, 1985
Cladotricha Gajewskaja, 1926
Parentocirrus Voss, 1997
Engelmanniella Foissner, 1982
Deviata Eigner, 1995

Table 11 Classification of kahliellid ciliates according to Jankowski (2007)

Family Kahliellidae Tuffrau, 1979
Cladotricha Gajewskaja, 1926
Deviata Eigner, 1995
Perisincirra Jankowski, 1979
Engelmanniella Foissner, 1982
Kahliella Corliss, 1960
Plesiotricha Dragesco, 1970
Neogeneia Eigner, 1995
Parakahliella Berger, Foissner et Adam, 1985
Fragmocirrus Foissner, 2000
Pseudokahliella Berger, Foissner et Adam, 1985

Table 12 Classification of kahliellid ciliates according to Lynn (2008)

Family Kahliellidae Tuffrau, 1979
Cladotricha Gajewskaja, 1926
Deviata Eigner, 1995
Engelmanniella Foissner, 1982
Kahliella Corliss, 1960
Neogeneia Eigner, 1995
Parakahliella Berger, Foissner and Adam, 1985
Plesiotricha Dragesco, 1970 (subj. syn. *Kahliella*)
Pseudokahliella Berger, Foissner and Adam, 1985
Trachelochaeta Šrámek-Husek, 1954
Wallackia Foissner, 1976
Incertae sedis in Family Kahliellidae
Banyulsella Dragesco, 1954
Fragmocirrus Foissner, 2000
Lacazea Dragesco, 1960
Pseudouroleptus Hemberger, 1985

Table 13 Classification of parakahliellid ciliates according to Eigner (1997) and Eigner (1999; adapted names in parenthesis)

Family Parakahliellidae Eigner, 1997
Neogeneia hortualis
Parakahliella macrostoma
Onychodromus quadricornutus
Kerona polyporum
Paraurostyla weissei
Parentocirrus hortualis
Amphisiellides illuvialis
Gastrostyla steinii
Onychodromus grandis
Coniculostomum monilata
Pattersoniella vitiphila
Histriculus muscorum (Sterkiella histriomuscorum)
Steinia sphagnicola
Cyrtohymena muscorum
Notohymena rubescens
Clara pustulata (Tetmemena pustulata)
Clara vorax (Tetmemena vorax)
Urosomoida agiliformis

4 Parasitism

There is no paper verifying that gonostomatids, kahliellids, or other taxa treated in this volume are parasitised by suctorians, a group which sometimes attacks oxytrichids and urostyloids (for reviews, see Berger 1999, 2006a). However, the small *Sphaerophrya terricola* Foissner, 1986 (20–30 µm across) feeds on *Gonostomum af-*

fine (Foissner 1986, p. 51). For reviews on suctorians, see Collin (1912), Kahl (1934), Matthes (1988), Dovgal (2002), Lynn & Small (2002), and Jankowski (2007).

The terricolous, holocarpic, and endobiotic lagenidiaceous fungus *Ciliomyces spectabilis* Foissner & Foissner, 1986[1] parasitises the resting cyst of *Kahliella simplex* (Foissner I. & Foissner W. 1985, 1986a, b; Foissner 1987a, p. 86; 1994, p. 210). The single-celled vegetative thallus is spherical, elongated, or lobed. Before the zoosporangium is formed, the vegetative thalli transform into rather thin hyphae (2–6 µm across), which are contorted and often link-like and occasionally branched. The mature sporangium is pear-shaped and about 22–30 × 30–44 µm in size[2]. The zoospore is elongated, about 6 × 3 µm, and posteriorly slightly tapered. Infection starts with encysted zoospores, which perforate the ciliate cyst wall by their germ tubes (Fig. 5a). For a detailed explanation of the complete life cycle of *Ciliatomyces spectabilis* (Fig. 5a–j), see Foissner & Foissner (1986a, b).

5 Ecology, Occurrence, and Geographic Distribution

Little is known about these topics for most species reviewed in this volume. In contrast to the oxytrichids and the urostyloids, which occur in all major biotopes (sea, freshwater, soil), most kahliellids and gonostomatids live (mainly) in terrestrial habitats; *Cladotricha* and *Apourosomoida* are more or less confined to highly saline habitats, *Pseudokahliella* and *Stenotricha* inhabit the sea, and only few species are limno-terrestrial (e.g., *Engelmanniella mobilis*) or likely confined to limnetic habitats (*Trachelochaeta bryophila*). The very low number of freshwater species explains why most species reviewed in the present volume and in volume 3 (Berger 2008) do not occur in the old literature, because Ehrenberg (1838), Claparède & Lachmann (1858), Stein (1859) and other authors studied mainly small, stagnant water bodies. For the same reason, no species is included in the list of biological indicators for water quality assessment (e.g., Foissner & Berger 1996, Berger & Foissner 2003); in addition, gonostomatids and kahliellids (usually) do not occur in ordinary sewage treatment plants (e.g., Curds 1975, Ganner et al. 2002, Berger et al. 2008, Berger 2009). Only *Deviata brasiliensis*, a species of uncertain phylogenetic position, has its type locality in a sewage treatment plant (Fig. 100a, b). The water-inhabiting species are, like most other hypotrichs, bottom dwellers creeping on, for example, debris, stones, or macrophytes; pelagic species are not described. Species found in the marine interstitial are summarised by Carey (1992) and Patterson et al. (1989). No parasitic or symbiotic species or genus is known, and likely no species is obligatorily anaerobic (Fenchel & Finlay 1995).

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[1] Foissner & Foissner (1995) found that *Ciliomyces* Foissner & Foissner, 1986 is a junior homonym and therefore introduced the replacement name *Ciliatomyces* Foissner & Foissner, 1995. The correct name of the species is now *Ciliatomyces spectabilis* (Foissner & Foissner, 1986) Foissner & Foissner, 1995.

[2] 22–20 × 30–44 µm in Foissner & Foissner (1986b, p. 44) is obviously a printer's error. I did not find the original notes, but I suppose that 22–30 × 30–44 µm is the correct ratio for a pear.

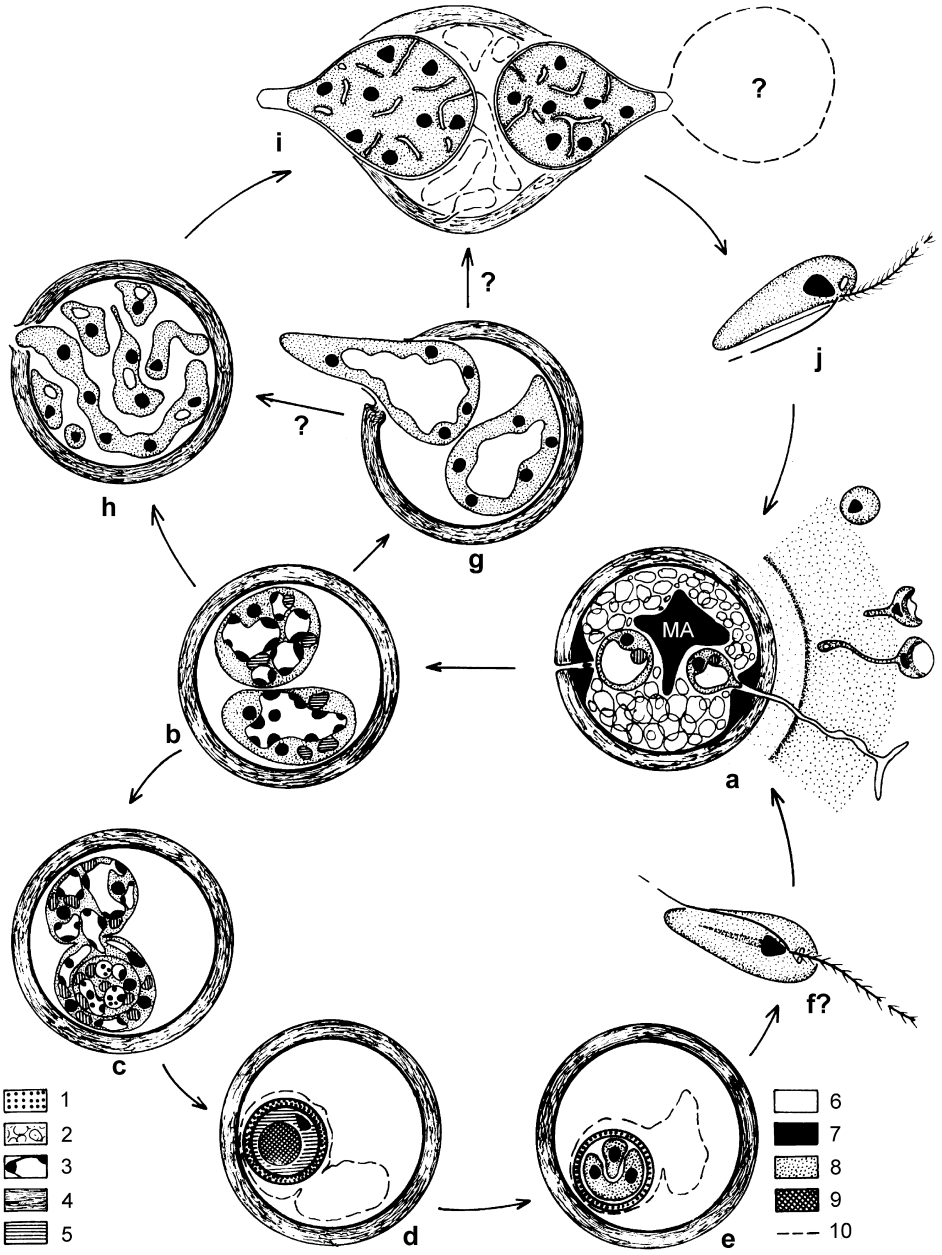

Fig. 5a–j Life cycle of *Ciliatomyces spectabilis*, a fungus parasitising the resting cyst of *Kahliella simplex* (from Foissner & Foissner 1986b). **a:** Infection. **b:** Vegetative thalli. **c–f:** Sexual reproduction. **g–j:** Asexual reproduction. Unknown stages or transitions are indicated by a question mark. The diplophase is probably confined to the oospore. All stages are shown in optical sections. Magnifications: about 560×, except zoospores: 2800×. MA = macronucleus, 1 = oospore, 2 = ciliate cytoplasm, 3 = vacuole with peripheral appositions, 4 = ciliate cyst wall, 5 = lipid, 6 = vacuole, 7 = nucleus, 8 = cytoplasm/mucus, 9 = reserve globule, 10 = empty cell wall/zoosporangial vesicle.

The name-bearing groups of the kahliellids (*Kahliella*, previously *Kahlia*) and the gonostomatids (*Gonostomum*) are already included in the review by Kahl (1932). By contrast, the discovery of most soil species reviewed in the current volume started cautious in the thirties of the past century mainly by Horváth (1932, 1934). Later, Foissner, Wilbert, Eigner, and several other workers provided many detailed studies including ontogenetic ones (see reference section). However, *Gonostomum affine* – likely the most common soil hypotrich (e.g., Foissner 1987a, 1998) – was already discovered by Stein (1859) in a limnetic habitat. Interestingly, this widespread species, which is – like most other hypotrichs – rather K- than r-selected, adapts poorly to changing environmental conditions as, for example, temperature (Lüftenegger et al. 1985).

The species discussed in the systematic section have basically the same food spectrum as other hypotrichs (for reviews, see Berger 1999, 2006a, 2008), that is, they feed on bacteria, cyanobacteria, algae (including diatoms), auto- and heterotrophic flagellates, and ciliates. Small metazoans (e.g., rotifers) are usually not ingested because most species are too small for such prey. The menu of the individual species is of course often much shorter than the list above. Some hypotrichs are likely specialists ingesting, for example, only/mainly bacteria.

Rather little is known about the geographic distribution of most species reviewed. The kahliellids and gonostomatids as such are likely distributed world-wide. Of course we are unable to say for hypotrichs, and ciliates in general, whether a certain group or species is endemic, confined to a certain biogeographic area, or cosmopolitan, because too few reliable records are published. The available data, however, indicate that at least some taxa have a restricted distribution. *Cladotricha* species, for example, are not reliable recorded from Africa. Probably, this halophile group is replaced by the likewise halophile *Apourosomoida* in this continent (see also Berger 2008). Perhaps the same is true for *Parakahliella* and the newly established *Afrokahliella*. *Circinella arenicola* (worm-like and cephalised; p. 317) and *Saudithrix terricola* (very large and very many cirri; p. 648) are eye-catching species. Since they have been recorded only once (Utah, USA) or twice (Saudi Arabia, China), it is very likely that they have a restricted distribution. When they would have a wide or even cosmopolitan range, we had to assume that they have been overlooked or misidentified all the time, an implausible explanation. Of course much more serious studies are needed to support or disprove such biogeographic hypotheses.

In the descriptions of the individual species most (all?) records published so far are mentioned. There is no doubt that in some cases the determinations are incorrect. Thus, records not substantiated by serious morphological data should be used with caution for biogeographic interpretations. As in other groups of hypotrichs, or ciliates and protists in general, many more species than reviewed in the present book exist because only few areas have been studied in detail outside of Europe, for example, the Namib desert (Foissner et al. 2002a, b), Australia (e.g., Blatterer & Foissner 1988, Wilbert 1995), or the Yellow Sea (Song et al. 2009). And even in Central

Europe, which is already well-investigated, new gonostomatids or kahliellids can be discovered (e.g., Eigner 1995, Foissner et al. 2005, Vd'ačný & Tirjaková 2006a).

6 Collecting, Culturing, Observing, and Staining of Hypotrichous Ciliates

A detailed description of these topics for all ciliates is given by Foissner (1991, 1993), Foissner et al. (1991, 1999, 2002a), Röttger (1995), and Röttger et al. (2009).

6.1 Collecting and Culturing

Most species treated in the present volume are terrestrial and/or limnetic; only few occur in marine habitats.

The most effective means for collecting and culturing gonostomatids, kahliellids, and other ciliates from soils and mosses is the non-flooded petri dish method as described by Foissner (1987a; see also Foissner 1993 and Foissner et al. 2002a). Here, 10–200 g of fresh or air-dried soil or litter sample are placed in a petri dish (10 to 20 cm across) and saturated, but not flooded, with distilled water. A ciliate, flagellate, and naked amoeba fauna, often very rich, develops within a few days. Inspection of the cultures on days 2, 4, 6, 10, 14, and 20 usually suffices. Subsequent inspections reveal only few species due to the effects of ciliatostasis (Lüftenegger et al. 1987). *Paraholosticha* and *Keronopsis* (reviewed in a later volume) species usually occur after few hours, the very common *Gonostomum affine* can be found also in old cultures. Several conditions influence the outcome of the method: (i) air-dried soil often yields more individuals and species than fresh soil, perhaps due to reduced microbiostasis; (ii) the sample should contain ample litter and plant debris and must be spread over the bottom of the petri dish in an at least 1 cm thick layer; (iii) the soil may not be flooded. Water should be added to the sample until 5–20 ml drains off when the petri dish is tilted and the soil is gently pressed with a finger. This run-off contains the protozoa and can be used for further preparations such as silver staining.

The methods for culturing hypotrichous ciliates are treated only briefly here as detailed culturing methods – if available – are provided in the species descriptions. Furthermore, the general procedures, as described, for instance, by Dragesco & Dragesco-Kernéis (1986), Finlay et al. (1988), Foissner et al. (1991, 2002a), Galtsoff et al. (1959), Hall (1964), Kidder (1964), Lee et al. (1985), Mayer (1981), Provasoli et al. (1958), and van Wagtendonk (1955), apply also to the hypotrichs.

In general, bacteriovorous hypotrichs thrive on various media (e.g., diluted lettuce and/or hay extracts, table waters [e.g., Volvic], tap water) enriched with a little dried yolk, rice grains, or crushed wheat grains to promote bacterial growth. Some predatory species grow well with small ciliates (e.g., species of the *Tetrahymena py-*

riformis complex, *Glaucoma scintillans*) as food. For marine species, artificial sea water (e.g., the supersoluble seasalt Biosal by Aqualine Buschke, Berg, Germany) can be used.

6.2 Observing Living Hypotrichs

Many physical and chemical methods have been described for retarding the movement of ciliates in order to observe structural details (for literature see Foissner 1991). Chemical immobilisation – for example, by nickel sulfate – or physical slowing down by increasing the viscosity of the medium (e.g., methyl cellulose) are rarely helpful. These procedures often change the shape of the cell or cause premortal alterations of various cell structures. The following simple method is therefore preferable: place about 0.5 ml of the raw sample on a slide and pick out (collect) the desired specimens with a micro-pipette under a compound microscope with low magnification (for example, objective 4:1, ocular 10×). If specimens are large enough, they can be picked out from a petri dish under a dissecting microscope. Working with micro-pipettes, the diameter of which must be adjusted to the size of the specimens, requires some training. Transfer the collected specimens, which are now in a very small drop of fluid, onto a slide. Apply small dabs of Vaseline (Petroleum jelly) to each of the four corners of a small cover glass (Fig. 6a; the four dabs can be also applied to the slide); it is useful to apply the jelly by an ordinary syringe with a thick needle. Place the cover glass on the droplet containing the ciliates. Look through the microscope and press gently on the vaselined corners with a mounted needle until ciliates are held firmly between slide and cover glass (Fig. 6b–d). As the pressure is increased the ciliates gradually become less mobile and more transparent. Hence, first the location of the main cell organelles (e.g., nuclear and oral apparatus, contractile vacuole) and then details (e.g., cortical granules, micronucleus) can easily be observed under low (100–400×) and high (1000×; oil immersion objective) magnification. The colour of the cortical granules and/or the cytoplasm must be studied with well-adjusted bright field.

The shape of the cells is of course altered by this procedure. Therefore, specimens taken directly from the raw culture with a large-bore (opening about 1 mm) Pasteur pipette must first be investigated under low magnification (100–400×), that is, without cover glass. Some species are too fragile to withstand handling with micro-pipette and cover glass trapping without deterioration. Investigation with low magnification also requires some experience, but it guarantees that the outline of undamaged cells are recorded. Video-microscopy is very useful at this point of investigation, especially for the registration of the swimming behaviour.

A compound microscope equipped with Normarski differential interference contrast optics is best for discerning the arrangement of the cirri and dorsal cilia in living hypotrichs. If not available, use bright-field. The nuclear apparatus is well-recognisable with differential interference contrast or phase-contrast when specimens are strongly squeezed.

Species that were not observed in life often cannot be identified after silver impregnation with certainty because important characters (e.g., size, shape, colour of cortical granules, colour of cytoplasm) are not known. As already mentioned above, the correct colour can only be seen with a well-adjusted bright field illumination.

6.3 Staining Procedures

There are many methods for staining ciliates, but only protargol silver impregnation yields (usually) good results in hypotrichs. Thus, familiarity with this method is an absolute prerequisite for the description of hypotrichs. It is thus described in detail. Simple, namely molecular, formulae are given for the chemicals used, since usually only these are found in the catalogues of the suppliers (e.g., Merck). Other silver impregnation methods (dry silver nitrate method, wet silver nitrate method, silver carbonate method), detailed literature, and some general instructions are to be found in the reviews by Foissner (1991, 1993), Foissner et al. (1991, 1999), and Mulisch & Welsch (2010).

Apart from silver impregnation, some other staining techniques are useful for taxonomic work with ciliates, especially the Feulgen nuclear reaction and supravital staining with methyl green-pyronin in order to reveal the nuclear apparatus and, respectively, the extrusomes.

6.3.1 Feulgen Nuclear Reaction

Descriptions of this method are to be found, for example, in Dragesco & Dragesco-Kernéis (1986) and Lee et al. (1985). The Feulgen reaction reveals the nuclear apparatus very distinctively, but, because these organelles usually stain well with protargol, it is seldom used for hypotrichs.

6.3.2 Supravital Staining with Methyl Green-Pyronin

This simple method was described by Foissner (1979). It is an excellent technique for revealing the mucocysts of most ciliates. Mucocysts are stained deeply and very distinctively blue or red, and can be observed in various stages of explosion because the cells are not killed instantly. The nuclear apparatus is also stained.

Procedure (after Foissner 1991)

1. Pick out desired ciliates with a micro-pipette and place the small drop of fluid in the centre of a slide.

2. Add an equally sized drop of methyl green-pyronin and mix the two drops gently by swivelling the slide.
Remarks: If ciliates were already mounted under the coverslip, add a drop of the dye at one edge of the coverslip and pass it through the preparation with a piece of filter paper placed at the other end of the coverslip.

3. Place a coverslip with vaselined corners on the preparation.
Remarks: Observe immediately. Cells die in the stain within 2 min. Mucocysts stain very quickly and many can be observed at various stages of explosion. To reveal the nuclear apparatus, cells should be fairly strongly squashed (= flattened). The preparation is temporary. After 5–10 min the cytoplasm often becomes heavily stained and obscures other details.

Reagents

1 g methyl green-pyronin (Chroma-Gesellschaft, Schmid GmbH and Co., Köngen/N., Germany)
add 100 ml distilled water
This solution is stable and can be used for years.

6.3.3 Protargol Methods

Protargol methods are indispensable for descriptive research on hypotrichs. The first procedures were provided by Kirby (1945), Moskowitz (1950), Dragesco (1962), and Tuffrau (1964, 1967), and many more modifications were subsequently proposed (see Foissner 1991 for references). Here, two variations which produce good results are described. These procedures work well with most ciliate species, but require at least 20 specimens. A single specimen cannot usually be handled successfully. Depending on the procedure used, protargol can reveal many cortical and internal structures, such as basal bodies, fibrillary systems, nuclear apparatus. The silverlines (which have no systematic value in the hypotrichs), however, never impregnate. The shape of the cells is usually well preserved in permanent slides, which is an advantage for the investigation, but makes photographic documentation more difficult. However, pictures as clear as those taken from wet silver carbonate impregnations can be obtained with the Wilbert modification (procedure B) if the cells are photographed prior to embedding in the albumen-glycerol.

Procedure A (after Foissner 1991)

The quality of the slides is usually adequate but frequently not as good as with the Wilbert modification. The latter demands more material and experience; inexperienced workers may easily lose all the material. As in all protargol methods, the pro-

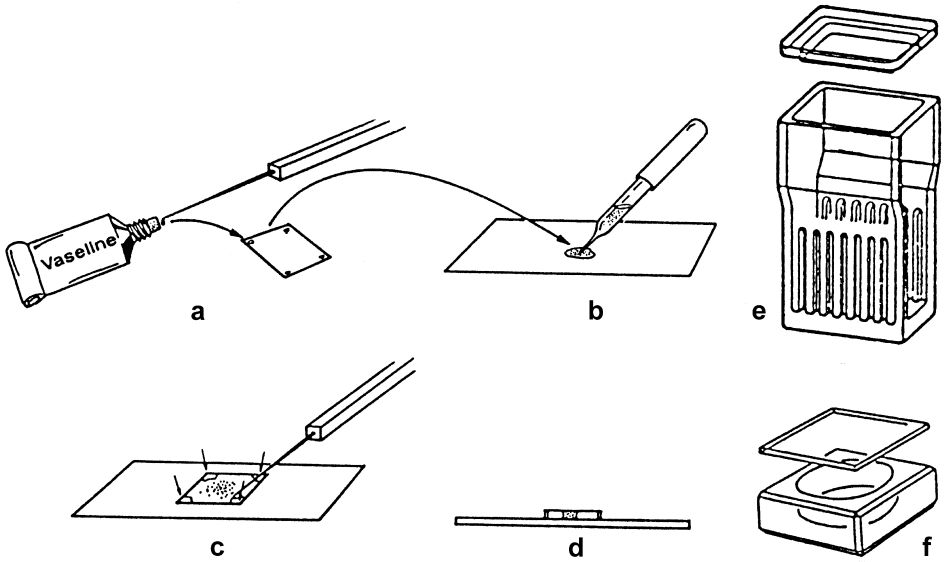

Fig. 6a–f Live observation and staining of urostyloid ciliates (from Foissner 1991). **a–d:** Preparation of slides for observing living ciliates. **e:** Staining jar for 8 and 16 (back to back) slides, respectively. **f:** Watch-glass for protargol procedure according to Wilbert.

cedure is rather time-consuming and complicated because subject to many factors. A centrifuge may be used for step 2; staining jars (Fig. 6e) are necessary for steps 6–16.

1. Fix organisms in Bouin's or Stieve's fluid for 10–30 min.
Remarks: The fixation time has little influence on the quality of the preparation within the limits given. Ratio fixative to sample fluid should be at least 2:1. Pour ciliates into fixative using a wide-necked flask in order to bring organisms in contact with the fixative as quickly as possible. Both fixatives work well but may provide different results with certain organisms. Stieve's fluid may be supplemented with some drops of 2% osmium tetroxide for better fixation of very fragile hypotrichs. This increases the stability of the cells but usually reduces their impregnability. Alternatively, 70% ethanol can be used for fixation (W. Foissner, pers. comm.).

2. Concentrate by centrifugation and wash organisms 3–4 times in distilled water.
Remarks: There are now two choices: either to continue with step 3, or to transfer the material through 30–50–70% alcohol into 70% alcohol (ethanol), where it remains stable for several years. Transfer preserved material back through the graded alcohol series into distilled water prior to continuing with the next step. Impregnability of preserved material may be slightly different.

3. Clean eight ordinary slides (or less if material is very scarce) per sample. The slides must be grease-free (clean with alcohol and flame).
Remarks: Insufficiently cleaned slides may cause the albumen to detach. Mark slides on back if several samples are prepared together. Alternatively you can use Super-Frost slides which are ready to use. In addition, these slides have a field enabling simple labelling with a pencil. Use staining jars with eight sections so that you can work with 16 slides simultaneously by putting them back to back (Fig. 6e).

4. Put one drop each of albumen-glycerol and concentrated organisms in the centre of a slide. Mix drops with a mounted needle and spread over the middle third.
Remarks: Use about equally sized drops of albumen-glycerol and suspended (in distilled water) organisms to facilitate spreading. The size of the drops should be adjusted so that the middle third of the slide is covered after spreading. Now remove sand, grains, etc. The thickness of the albumen layer should be equal to that of the organisms. Some thicker and thinner slides should, however, also be prepared because the thickness of the albumen layer greatly influences the quality of the preparation. Cells may dry out and/or shrink if the albumen layer is too thin; if it is too thick, it may detach, or the cells may become impossible to study with the oil immersion objective.

5. Allow slides to dry for at least 2 h at room temperature.
Remarks: We usually dry slides overnight, that is, for about 12 h. However, slides may be allowed to dry for up 24 h, but no longer if quality is to be maintained. Oven-dried (2 h at 60 °C) slides are usually also of poorer quality.

6. Place slides in a staining jar (Fig. 6e) filled with 95% alcohol (ethanol) for 20 to 30 min. Place a staining jar with protargol solution into an oven (60 °C).
Remarks: Slides should not be transferred through an alcohol series into concentrated alcohol as this causes the albumen layer to detach! Decrease hardening time to 20 min if albumen is already rather old and/or not very sticky.

7. Rehydrate slides through 70% alcohol and two distilled water steps for 5 min each.

8. Place slides in 0.2% potassium permanganate solution. Remove first slide (or pair of slides) after 60 s and the rest at 15 s intervals. Collect slides in a staining jar filled with distilled water.
Remarks: Bleaching is by permanganate and oxalic acid (step 9). The procedure described above is necessary because each species has its optimum bleaching time. The sequence in which slides are treated should be recorded because the immersion time in oxalic acid must be proportional to that in the permanganate solution. The albumen layer containing the organisms should swell slightly in the permanganate solution and the surface should become uneven. If it remains smooth, the albumen is too sticky and this could decrease the quality of the impregnation. If the albumen swells

strongly, it is possibly too weak (old) and liable to detach. Use fresh $KMnO_4$ solution for each series.

9. Quickly transfer slides to 2.5% oxalic acid. Remove first slide (or pair of slides) after 160 s, the others at 20 s intervals. Collect slides in a staining jar filled with distilled water.
Remarks: Same as for step 8! Albumen layer becomes smooth in oxalic acid.

10. Wash slides three times in distilled water for 3 min each.

11. Place slides in warm (60 °C) protargol solution and impregnate for 10–15 min at 60 °C.
Remarks: Protargol solution can be used only once.

12. Remove staining jar with the slides from the oven and allow to cool for 10 min at room temperature.
Remarks: In the meantime organise six staining jars for developing the slides: distilled water – distilled water – fixative (sodium thiosulfate) – distilled water – 70% alcohol – 100% alcohol (ethanol).

13. Remove the first slide from the protargol solution and drop some developer on the albumen layer. Move slide gently to spread developer evenly. As soon as the albumen turns yellowish, pour off the developer, dip slide in the first two distilled water steps for about 2 s each and stop development by submerging the slide in the fixative (sodium thiosulfate), where it can be left for 1–5 min.
Remarks: Now control impregnation with the compound microscope. The impregnation intensity is sufficient if the infraciliature is just recognisable. The permanent slide will be too dark if the infraciliature is distinct at this stage of the procedure! The intensity of the impregnation can be controlled by the concentration of the developer and the time of development. 5–10 s usually suffice for the diluted developer! Development time increases with bleaching time. Therefore commence development with those slides which were in the bleaching solutions for 60 and 120 s, respectively. The thinner the albumen layer, the quicker the development.

14. Collect slides in the fixative (sodium thiosulfate) and transfer to distilled water for up to 5 min.
Remarks: Do not wash too long; the albumen layer is very fragile and detaches rather easily!

15. Transfer slides to 70% – 100% – 100% alcohol for 5 min each.

16. Clear by two 10 min transfers through xylene.

17. Mount in synthetic neutral mounting medium.

Remarks: Do not dry slides between steps 16 and 17! Mounting medium should be rather viscous to avoid air-bubbles being formed when solvent evaporates during drying. If air-bubbles develop in the mounted and hardened slide, re-immerse in xylene for some days until the coverslip drops off. Remount using a more viscous medium and remove possible sand grains protruding from the gelatine. Usually, some air-bubbles are found immediately after mounting; these can be pushed to the edge of the coverslip with a finger or mounted needle. The preparation is stable.

Reagents

a) Bouin's fluid (prepare immediately before use; components can be stored)
15 parts saturated, aqueous picric acid ($C_6H_3N_3O_7$; preparation: add an excess of picric crystals to, for example, 1 litre of distilled water; shake solution several times within a week; some undissolved crystals should remain; filter before use)
5 parts formalin (HCHO; commercial concentration, about 37%)
1 part glacial acetic acid (= concentrated acetic acid; $C_2H_4O_2$)

b) Stieve's fluid (slightly modified; prepare immediately before use; components can be stored)
38 ml saturated, aqueous mercuric chloride (dissolve 60 g $HgCl_2$ in 1 litre of boiling distilled water)
10 ml formalin (HCHO; commercial concentration, about 37%)
3 ml glacial acetic acid (= concentrated acetic acid; $C_2H_4O_2$)

c) Albumen-glycerol (2–4 month stability)
15 ml egg albumen
15 ml concentrated (98–100%) glycerol ($C_3H_8O_3$)

Pre-treatment of the egg albumen and preparation of the albumen-glycerol: separate the white carefully from the yolk and embryo of three eggs (free range eggs are preferable to those from battery chickens, whose egg white is less stable and sticky). Shake the white by hand (do not use a mixer!) for some minutes in a narrow-mouthed 250 ml Erlenmeyer flask until a stiff white foam is formed. Allow the flask to stand for about 1 min. Then pour the viscous rest of the egg white in a second Erlenmeyer flask and shake again until a stiff foam is formed. Repeat until most of the egg white is either stiff or becomes watery; usually 4–6 Erlenmeyer flasks of foam are obtained. Leave all flasks undisturbed for about 10 min and discard the watery albumen from the last flask. During this time a glycerol-like fluid percolates from the foam. This fluid is collected and used. Add an equal volume of concentrated glycerol and a small thymol crystal ($C_{10}H_{14}O$) for preservation to the mixture. Mix by shaking gently and pour mixture into a small flask. Leave undisturbed for two weeks. A whitish slime settles at the bottom of the flask. Decant the clear portion, discard slime and thymol crystal. A "good" albumen-glycerol drags a short thread when touched with a needle. The albumen is too thin (not sticky enough) or too old

if this thread is not formed. Fresh albumen which is too thin may be concentrated by leaving it open for some weeks so that water can evaporate. If the albumen is too sticky, which may cause only one side of the organisms to impregnate well, it is diluted with distilled water or old, less sticky albumen to the appropriate consistency. The preparation of the albumen-glycerol must be undertaken with great care because much depends on its quality. Unfortunately, all commercial products which have been tried detach during impregnation. A somewhat simpler method to produce the albumen-glycerol is described by Adam & Czihak (1964, p. 274): the white of one or two fresh chicken egg(s) and the same amount of concentrated glycerol are well stirred to a homogenous, thick fluid (a magnetic stirrer can be used). Then filter through cotton wool. Add a small thymol crystal to the filtrate. The albumen-glycerol can be used right away.

d) 0.2% potassium permanganate solution (stable for about 1 d)
0.2 g potassium permanganate ($KMnO_4$) are dissolved in 100 ml distilled water

e) 2.5% oxalic acid solution (stable for about 1 d)
2.5 g oxalic acid ($C_2H_2O_4 \cdot 2H_2O$) are dissolved in 100 ml distilled water

f) 0.4–0.8% protargol solution (stable for about 1 d)
100 ml distilled water
add 0.4–0.8 g protargol
Remarks: Use light-brown "protargol for microscopy" (for example, Merck's "Albumosesilber für die Mikroskopie" or "Proteinate d'Argent", Roques, Paris, France). Some dark-brown, cheaper products do not work! Sprinkle powder on the surface of the water in the staining jar and allow to dissolve without stirring.

g) Developer (mix in sequence indicated; sodium sulphite must be dissolved before hydroquinone is added)
95 ml distilled water
5 g sodium sulphite (Na_2SO_3)
1 g hydroquinone ($C_6H_6O_2$)
Remarks: This recipe yields the stock solution which is stable for some weeks and should be used undiluted for certain ciliates (step 13). Usually, however, it must be diluted with tap water in a ratio of 1:20 to 1:50 to avoid too rapid development and one-sided impregnation of the organisms. Freshly prepared developer is usually inadequate (the albumen turns greenish instead of brownish). The developer should thus be prepared from equal parts of fresh and old (brown) stock solutions. Take great care with the developer as its quality contributes highly to that of the slides. If the developer has lost its activity (which is not always indicated by a brown colour!) the silver is not or only insufficiently reduced and the organisms stain too faintly. A fresh developer should therefore be prepared for each "impregnation week", and some old developer kept. Fresh developer can be artificially aged by adding some sodium carbonate (Na_2CO_3). However, better results are obtained with air-aged solu-

tions, that is, by a developer which has been kept uncovered for some days in a wide-mouthed bottle. It first turns yellowish, then light brown (most effective), and later dark brown and viscous (at this stage the developer has lost most of its activity, but is still suitable for artificial ageing of fresh developer = 1:1 mixture mentioned above).
During the last years, we obtained very good slides with the low-speed developer used by Fryd-Versavel (pers. comm. to W. Foissner). It is composed of 7 g boric acid, 1.5 g hydroquinone, 10 g sodium sulphite, and 75 ml acetone, all solved, one by one, in 420 ml distilled water. This developer is stable for some weeks and should be used only once. Pour developer into a staining jar and immerse slides, one by one, controlling impregnation intensity after 30–60 s. Usually, developing is finished within 1–5 min (if not, double protargol concentration because slides should not be too long in the developer, as the albumen may detach). The further procedure is as described above (steps 14–17).
In many cases commercial paper developers (for example, Ilford Multigrade) yield very good results.

h) Fixative for impregnation (stable for several years)
25 g sodium thiosulfate ($Na_2S_2O_3 \cdot 5H_2O$) are dissolved in 1000 ml distilled water

Procedure B (after Wilbert 1975 and Foissner 1991)

This modification produces excellent results but demands much experience. Manipulate large cells with micropipettes in a watch-glass, whereas the centrifuge is used for steps 1–4, 7, 8 if cells are smaller than about 150 µm. The watch-glass method is used when there are only few specimens of larger cells; thus an attempt is worthwhile even if only 20 cells are available. The organisms are very soft after development and fixation, and are thus easily compressed between slide and coverslip, which greatly facilitates photographic documentation.

1. Fix organisms as described in protargol procedure A.

2. Wash and, if so desired, preserve organisms as described in protargol procedure A.
Remarks: Wash cells either in the centrifuge (small species) or in a watch-glass (Fig. 6f). To change fluids allow cells to settle on bottom of watch-glass and remove supernatant with a micro-pipette under the dissecting microscope; concentrate cells in the centre of the watch-glass by gentle swirling.

3. Leave organisms in a small amount of distilled water and add, drop by drop, diluted sodium hypochlorite (NaClO) and bleach for about 1–3 min under the dissecting microscope (for small specimens, various concentrations of NaClO can be applied in centrifuge tubes, keeping the reaction time constant, for example, 1 min).
Remarks: This is the critical step in this modification. If bleaching is too strong or too weak all is lost: cells either dissolve or do not impregnate well. Systematic in-

vestigations showed that not the bleaching time but the amount of active chloride in the sodium hypochlorite and the pre-treatment of the cells (fixation method, fresh or preserved material) are decisive for the quality of the preparation. Different species need different concentrations. Unfortunately, the concentration of active chloride in the commercial products varies (10–13%) and is dependent on the age of the fluid. It is thus impossible to provide more than only a few guidelines: 100 ml distilled water plus 0.2–0.4 ml NaClO (if product is fresh and cells were not stored in alcohol) or 100 ml distilled water plus 0.5–1.6 ml NaClO (if product is older and cells were stored in alcohol). The transparency of the cells under the dissecting microscope may serve as a further indicator: fixed, unbleached cells appear dark and opaque, whereas accurately bleached cells are almost colourless and rather transparent (depends, however, also on size and thickness of the cell). Thus, increase the concentration of sodium hypochlorite stepwise if cells appear too dark with the recommended concentrations. We routinely start with three different hypochlorite concentrations if enough material is available.

4. Wash organisms at least three times with distilled water and finally once in the protargol solution.
Remarks: Wash thoroughly, especially when fluids are changed with micro-pipettes, because even the slightest traces of the sodium hypochlorite disturb impregnation.

5. Transfer to 1% protargol solution and impregnate for 10–20 min at 60 °C.
Remarks: This and the next step should be carried out in a watch-glass even for material which is otherwise manipulated with the centrifuge. The impregnation time depends on the kind of material and the degree of bleaching. Check the progress of impregnation every 3–4 min under the compound microscope by picking out a few cells with the micro-pipette under the dissecting microscope; add these to one drop of developer. Dilute developer and/or interrupt development of adding a little fixative (sodium thiosulfate) if impregnation is strong enough.

6. Remove most of the protargol solution with a micro-pipette and add some drops of developer to the remainder containing the organisms.
Remarks: Fresh, undiluted developer is usually used (but see step 5). Control development in compound or dissecting microscope. As soon as the infraciliature becomes faintly visible, development must be stopped by adding a few drops of sodium thiosulfate. Judging the right moment is a question of experience; the permanent slide will be too dark if the infraciliature is very distinct at this stage of the procedure! Generally: if bleaching was correct, specimens cannot be over-impregnated.

7. Stabilise the impregnation by two, approximately 5-minute transfers through sodium thiosulfate.
Remarks: The developer need not be removed before fixation. For small species this and the next step can be carried out in a centrifuge. Larger species must be manipulated with micro-pipettes because cells become very fragile and would be damaged

in a centrifuge. Cells are very soft at this stage and can thus be easily compressed and photographed. Transfer some of the more darkly impregnated specimens with a very small amount of the fixative onto a clean slide using a micro-pipette and cover with a coverslip. Organisms are usually flattened by the weight of the coverslip; excess fluid my be removed from the edge of the coverslip with a piece of filter paper. Frequently, even better micrographs are obtained if specimens are flattened before fixed with sodium thiosulphate; that is, together with some developer.

8. Wash very thoroughly in distilled water (three times with the centrifuge; 7–10 times in watch-glass with micro-pipettes). Finally remove as much of the water as possible.
Remarks: Even the slightest traces of the fixative destroy the impregnation within a few days or weeks.

9. Smear a moderately thick layer of albumen-glycerol on a clean slide with a finger. Drop impregnated, washed cells on the albumised slide with a large-bore pipette (opening about 1 mm) and dry preparation for at least 2 h.
Remarks: The cells are too fragile to be spread with a needle. With much care it is possible to orientate cells using a mounted eyelash. Commercial albumen-glycerol can be used.

10. Harden albumen by two 10-minute transfers through concentrated alcohol (ethanol).
Remarks: This and the next step are best carried out in staining jars. The albumen layer turns milky and opaque.

11. Clear by two 5-minute transfers through xylene.
Remarks: The albumen layer turns transparent.

12. Mount in synthetic neutral mounting medium.
Remarks: Do not dry slides between steps 11 and 12! Mounting medium should be rather viscous to avoid air-bubbles being formed when solvent evaporates during drying. If air-bubbles develop in the mounted and hardened slide, re-immerse in xylene for some days until the coverslip drops off. Remount using a more viscous medium and remove possible sand grains protruding from the albumen. Usually, some air-bubbles are found immediately after mounting; these can be pushed to the edge of the coverslip with a finger or mounted needle. The preparation is stable.

Reagents

If not stated otherwise, the same reagents as in the protargol procedure A are to be used (see above).

6.4 Preparation for Scanning Electron Microscopy

Hypotrichs cannot usually be identified solely by scanning electron microscopy because only a limited number of characters is revealed. However, this method is useful in that it allows a three-dimensional view of the object, as well as for documenting details which are difficult to reveal with other methods. For a detailed instruction of preparation for scanning electron microscopy, see Foissner (1991, 1993), Foissner et al. (1991, 1999), and other textbooks.

7 Species Concept and Nomenclature

7.1 Species Concept

The species/subspecies concept used in the present book is the same as described by Foissner et al. (2002a). Briefly, we usually apply the "morphospecies" concept as basically defined by Nixon & Wheeler (1990): "A species is the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)." That is, two populations are considered as belonging to two different species if they differ from each other in at least one "important" morphological feature, for example, number of macronuclear nodules or presence/absence of cortical granules. Of course, there is no strict consensus about the importance of various features and, unfortunately, for many species several features (e.g., presence/absence of cortical granules or caudal cirri; number of dorsal kineties; length of dorsal bristles; exact arrangement of cirri) are not known, making revisions rather difficult. Sometimes it is a matter of taste whether or not two species are synonymised. To overcome these difficulties I have kept the descriptions and the ecological data of synonyms separate, especially when they do not fit in all important details.

The presence/absence of a certain cirral group (e.g., caudal cirri, transverse cirri) is generally considered as diagnostic feature to characterise supraspecific taxa. However, characteristics of the cirral pattern are certainly not the sole source to elucidate the phylogenetic relationships. In the Oxytrichidae the consistence of the cell (flexible vs. rigid), the presence/absence of cortical granules, and the relative length (i.e., a quantitative feature!) of the adoral zone have been successfully used to characterise the Stylonychinae (Berger & Foissner 1997, Berger 1999), a group supported by all molecular analyses. Moreover, relevant molecular markers will significantly increase our knowledge on the phylogeny of hypotrichs.

For a discussion of the advantages and disadvantages of various species concepts, see textbooks on evolution (e.g., Ax 1984, 1995, Wägele 2001, Weisse 2008, Wiens 2000) and references cited by Foissner et al. (2002a, p. 35).

7.2 Notes on Nomenclature

In the case of nomenclatural problems, the International Code of Zoological Nomenclature has been consulted, depending on the date when the paper was published (ICZN 1964, 1985, 1999). For explanation of nomenclatural terms (e.g., nomen nudum, holotype), see the glossary of the ICZN (1999) or various textbooks (e.g., Corliss 1979, Lincoln et al. 1985, CBE 1996, Westheide & Rieger 1996, Winston 1999, Lynn 2008).

I tried to explain the origin and meaning of the scientific names using, inter alia, the ICZN (1985, 1999), Brown (1954), Werner (1972), Hentschel & Wagner (1996), Winston (1999), and Latin/German dictionaries. Likely less than 50% of the original descriptions contain an etymology section. The gender of ciliate genus-group names can be found, inter alia, in the valuable catalogue by Aescht (2001). I did not consult a Latin/Greek linguist; thus, improprieties cannot be excluded.

Note that in the reviews by Kahl (1932, 1933) only few species of gonostomatids and kahliellids are included. Most species reviewed in the present monograph are not treated in his papers because they have been discovered just in the last decades during the systematic investigation of soil from throughout the world (for reviews, see Foissner 1987a, 1998, Foissner et al. 2002a).

For authorship and date of hypotrichs not reviewed in the present book, see Berger (1999, 2001, 2006a, 2008). For a bibliography on hypotrichs and euplotids, see Berger (2006b).

As in the first three volumes of the revision of hypotrichs (Berger 1999, 2006a, 2008), higher taxa (e.g., Oxytrichidae, Stylonychinae, Urostyloidea, Gonostomatidae, Kahliellidae) are not provided with categories (e.g., family, order, class), simply because categories do not contain information and cannot be defined objectively (e.g., Mayr 1975, p. 89; Ax 1995, Westheide & Rieger 1996, Wägele 2001).[1] Recently, Adl et al. (2005) also refrained from the futile assignment of categories in their higher level classification of protists. For example, the taxon Hypotricha was established as order by Stein (1859). Since then it also attained the categories suborder, subclass, and even class (e.g., Small & Lynn 1985, Tuffrau & Fleury 1994; for review, see Berger 2001). However, to avoid inflation of names I use those which are available. When more than one name is available for a certain taxon I use the older one, unless the composition of the taxon was distinctly modified. Therefore the "defined" endings (ICZN 1999, Article 29.2; e.g., -idae, -inae) have **no meaning** in the present book.

[1] The sole higher level category (above the taxon and category species) which is used in the monograph is the genus, simply because it is part of the species name and therefore necessary for nomenclatural reasons. See Ax (1995, p. 18) for detailed explanation of the terms taxon (e.g., Mammalia, Ciliophora, *Paramecium*, *Homo sapiens*), category (e.g., genus, family, order, subclass), and rank (as a result of a dichotomous splitting there are only two taxa of equal rank within a monophyletic group). For example, in Fig. 6a in Berger (2008), the Perilemmaphora (Oligotricha + Hypotricha) and the Discocephalidae have the same rank.

7.3 Summary of New Taxa and Nomenclatural Acts

In the present book and in Li et al. (2010), a paper also supported by the present FWF-project, the nomenclatural acts listed below have been undertaken. Within the sections, the taxa are arranged alphabetically. All names refer to hypotrichous ciliates, unless otherwise indicated.

New combinations: *Afrokahliella binucleata* (Foissner, Agatha & Berger, 2002) comb. nov. (p. 449; basionym *Parakahliella binucleata* Foissner, Agatha & Berger, 2002); *Afrokahliella halophila* (Foissner, Agatha & Berger, 2002) comb. nov. (p. 440; basionym *Parakahliella halophila* Foissner, Agatha & Berger, 2002); *Afrokahliella namibicola* (Foissner, Agatha & Berger, 2002) comb. nov. (p. 434; basionym *Parakahliella namibicola* Foissner, Agatha & Berger, 2002); *Apogastrostyla rigescens* (Kahl, 1932) Li, Huang, Song, Shin, AL-Rasheid & Berger, 2010 (p. 197; basionym *Oxytricha (Tachysoma) rigescens* Kahl, 1932); *Apogastrostyla szaboi* (Wilbert & Song, 2005) Li, Huang, Song, Shin, AL-Rasheid & Berger, 2010 (p. 208; basionym *Hemigastrostyla szaboi* Wilbert & Song, 2005); *Apourosomoida elongata* (Ruinen, 1938) comb. nov. (p. 687; basionym *Cladotricha elongata* Ruinen, 1938); *Apourosomoida kahli* (Ruinen, 1938) comb. nov. (p. 689; basionym *Cladotricha kahli* Ruinen, 1938); *Apourosomoida variabilis* (Ruinen, 1938) comb. nov. (p. 690; basionym *Cladotricha variabilis* Ruinen, 1938); *Deviata quadrinucleata* (Dragesco, 2003) comb. nov. (p. 588; basionym *Kahliella quadrinucleata* Dragesco, 2003); *Deviata spirostoma* (Alekperov, 1988) comb. nov. (p. 597; basionym *Kahliella spirostoma* Alekperov, 1988); *Echinomeseres macdonaldi* (Ludwig, 1893) comb. nov. (p. 352; basionym *Meseres macdonaldi* Ludwig, 1893; Echinodermata); *Gonostomum terrestre* (Alekperov, 2005) comb. nov. (p. 164; basionym *Trachelochaeta terrestris* Alekperov, 2005); *Neowallackia franzi* (Foissner, 1982) comb. nov. (p. 281; basionym *Gonostomum franzi* Foissner, 1982); *Kahliella simplex* (Horváth, 1934) comb. nov. (p. 367; basionym *Kahlia simplex* Horváth, 1934); *Neowallackia ghangriai* (Kamra, Kumar & Sapra, 2008) comb. nov. (p. 295; basionym *Paragonostomum ghangriai* Kamra, Kumar & Sapra, 2008); *Neowallackia petergofi* (Alekperov, 2005) comb. nov. (p. 298; basionym *Trachelochaeta petergofi* Alekperov, 2005); *Rigidohymena candens* (Kahl, 1932) comb. nov. (p. 548; basionym *Oxytricha (Steinia) candens* Kahl, 1932); *Rigidohymena inquieta* (Stokes, 1887) comb. nov. (p. 548; basionym *Histrio inquietus* Stokes, 1887); *Rigidohymena quadrinucleata* (Dragesco & Njine, 1971) comb. nov. (p. 548; basionym *Steinia quadrinucleata* Dragesco & Njine, 1971); *Rigidohymena tetracirrata* (Gellért, 1942) comb. nov. (p. 548; basionym *Steinia tetracirrata* Gellért, 1942).

New subgenus: *Paragonostomum (Bigonostomum)* subgen. nov. (p. 184; type species *Paragonostomum multinucleatum* Foissner, Agatha & Berger, 2002).

New genera: *Afrokahliella* gen. nov. (p. 432; type species *Parakahliella namibicola* Foissner, Agatha & Berger, 2002); *Apogastrostyla* Li, Huang, Song, Shin, AL-Rasheid & Berger, 2010 (p. 196; type species *Oxytricha (Tachysoma) rigescens* Kahl, 1932); *Neowallackia* gen. nov. (p. 280; type species *Gonostomum franzi* Foissner, 1982); *Rigidohymena* gen. nov. (p. 547; type species *Steinia tetracirrata* Gellért, 1942).

New ranks: *Paragonostomum (Bigonostomum) binucleatum* Foissner, Agatha & Berger, 2002 (p. 192; basionym *Paragonostomum binucleatum* Foissner, Agatha & Berger, 2002); *Paragonostomum (Bigonostomum) multinucleatum* Foissner, Agatha & Berger, 2002 (p. 185; basionym *Paragonostomum multinucleatum* Foissner, Agatha & Berger, 2002); *Paragonostomum (Paragonostomum)* Foissner, Agatha & Berger, 2002 nov. stat. (p. 176; type species *Paragonostomum caudatum* Foissner, Agatha & Berger, 2002); *Paragonostomum (Paragonostomum) caudatum* Foissner, Agatha & Berger, 2002 (p. 176; basionym *Paragonostomum caudatum* Foissner, Agatha & Berger, 2002); *Paragonostomum (Paragonostomum) rarisetum* Foissner, Agatha & Berger, 2002 (p. 183; basionym *Paragonostomum rarisetum* Foissner, Agatha & Berger, 2002).

New names: *Echinomeseres* nom. nov. (p. 352; replacement name for *Meseres* Ludwig, 1893; type species *Meseres macdonaldi* Ludwig, 1893; Echinodermata).

Neotypifications: *Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982 (p. 502); *Kahliella simplex* (Horváth, 1934) comb. nov. (p. 367).

Corrected names: *Gonostomum gonostomoidum* (Hemberger, 1985) Berger, 1999 (p. 158); *Strongylidium arenicolum* Dragesco, 1953 (p. 681); *Tachysoma multinucleatum* Gong & Choi, 2007 (p. 209 in Li et al. 2010); *Trachelochaeta petergofi* Alekperov, 2005 (p. 298; fixed as correct original spelling); *Urosoma macrostomum* Gellért, 1957 (p. 168).

New synonyms: *Cladotricha edaphoni* Wilbert, 1995 is synonymous with *Cladotricha australis* Blatterer & Foissner, 1988 (p. 263). The Cladotrichidae Small & Lynn, 1985 are synonymous with the Gonostomatidae Small & Lynn, 1985 (p. 51, 54). *Gonostomum andoi* Shibuya, 1929 is synonymous with *Gonostomum strenuum* (Engelmann, 1862) Sterki, 1878 (p. 146). *Gonostomum singhii* Kamra, Kumar & Sapra, 2008 is synonymous with *G. affine* (Stein, 1859) Sterki, 1878 (p. 69). *Kahliella multiseta* Dragesco, 1970 is synonymous with *Kahliella simplex* (Horváth, 1934) comb. nov. (p. 367). *Uroleptus elongatus* Fernandez-Leborans, 1981 is a supposed synonym of *Deviata abbrevescens* Eigner, 1995 (p. 574).

Reactivated taxa: Gonostomatidae Small & Lynn, 1985 (p. 51); *Urosoma macrostomum* Gellért, 1957 (p. 168).

7.4 Deposition of Slides

If mentioned in the individual papers, the site(s) where the slide(s) (holotype; paratype; neotype; voucher) has (have) been deposited, is (are) given in the corresponding entry of the list of synonyms. For a detailed list of type specimens deposited in the collection "diverse invertebrates (except insects)" of the Biology Centre Linz (LI) in Upper Austria (= Oberösterreichisches Landesmuseum, = Upper Austrian Museum), see Aescht (2003, 2008; also available at www.biologiezentrum.at). Slides used for original observations are also deposited in this collection.

B Systematic Section

This volume is about the Gonostomatidae, the Kahliellidae, and several genera of uncertain phylogenetic position. With the key below and the subsequent keys all species reviewed in this book can be identified. There are two relatively easily recognisable features (gonostomatid oral apparatus; widely spaced cirri) indicating that a certain species is included in this revision. If one of the following points applies to your specimen/population you have a good chance of finding it in this volume.

- Oral apparatus in *Gonostomum*-pattern, that is, adoral zone not formed like a question mark, but mainly running along left anterior body margin with proximal portion knee-shaped extending towards cell midline; paroral composed of few, widely spaced cilia (Gonostomatidae; Fig. 3a, 7a–h, 24a–d)
- Some cirral rows with widely or very widely spaced cirri (Kahliellidae; e.g., Fig. 4a, b, arrows; 81a, 82c)
- Slender or wide species with few to many longitudinal frontoventral rows (e.g., *Orthoamphisiella*, *Saudithrix*, *Pseudokahliella*; Fig. 105a, e, 108a, f, 109a, f)
- Slender species from saline habitats with postoral cirri (*Apourosomoida*; Fig. 112a, 113a, 114a and Berger 2008, p. 514)
- Very slender, worm-like species with very short (6–16% of body length) adoral zone (e.g., *Circinella*, *Engelmanniella*; e.g., Fig. 57a, f, 86a, 87a)

The ventral cirral pattern of representatives of all genera treated in this book are summarised on the following plates (Fig. 7a–h, 8a–h, 9a–h). A key to all hypotrich genera and higher taxa will be provided in the last volume of the series.

The characterisation of the genera is rather detailed and often somewhat redundant, that is, contains features characteristic for the superordinated higher taxa. This extensive style is preferred before a short version because the higher level classification of several genera is rather uncertain.

Key to the Taxa Treated in Present Book

Before you start with the key you should familiarise yourself with the main morphological terms (see chapter 1 of general section, but also Berger 1999, 2006a, 2008, Foissner & AL-Rasheid 2006). Some key features (e.g., number of dorsal kineties, presence/absence of dorsomarginal kineties, caudal cirri, transverse cirri [must not be confused with caudal cirri or marginal cirri!]) are rather difficult to recognise in life, especially in species with a slender or posteriorly narrowed body. Thus, protargol preparations are needed for a reliable identification. Note that some genera are

H. Berger, *Monograph of the Gonostomatidae and Kahliellidae (Ciliophora, Hypotricha)*, Monographiae Biologicae 90, DOI 10.1007/978-94-007-0455-8_2,
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included twice because they cannot be assigned to a single character state unambiguously. If you are insecure at a certain couplet follow both leads, or keep in mind that your specimen or population can be a new species of a known genus or even a new representative of a new genus.

1 Saline habitats (sea, salt lake, brine, saline soil)[1]. **2**
- Non-saline habitats (limnetic habitats, non-saline soil)[1]. **5**

2 Oral apparatus gonostomatid (e.g., Fig. 3a, 7g, 9a). **3**
- Oral apparatus not as above (e.g., Fig. 9c). **4**

3 Postoral ventral cirri and (inconspicuous) transverse cirri present; long frontoventral row(s) lacking (e.g., Fig. 9f). . . . . *Apourosomoida* (p. 684 and Berger 2008, p. 514)
- Postoral ventral cirri and transverse cirri lacking; one or two long frontoventral rows present (Fig. 7g). . . . . *Cladotricha* (p. 235)

4 (2) Body slender, more or less distinctly cephalised; in total two long cirral rows present; transverse cirri present (Fig. 9e). . . . . *Stenotricha* (p. 680)
- Body wide elliptical, not cephalised; in total about 7–15 long cirral rows present; transverse cirri lacking (Fig. 9c). . . . . *Pseudokahliella* (p. 662)

5 (1) Adoral zone of membranelles gonostomatid (Fig. 7a–h, 8a) **6**
- Adoral zone of membranelles not as above (e.g., Fig. 8b, 9h). **8**

6 Dorsomarginal kinety lacking (e.g., Fig. 18c). . . . . Gonostomatidae (p. 51)
- Dorsomarginal kinety present (e.g., Fig. 4b, kinety 4). **7**

7 Frontal-ventral-transverse cirri arranged in 18-cirri pattern (e.g., Fig. 128n in Berger 1999). . . . . *Urosoma*[2] (Berger 1999, p. 396)
- Frontoventral cirri arranged in longitudinal rows, partially with widely spaced cirri (e.g., Fig. 4a, b). . . . . *Kahliella* (p. 347)

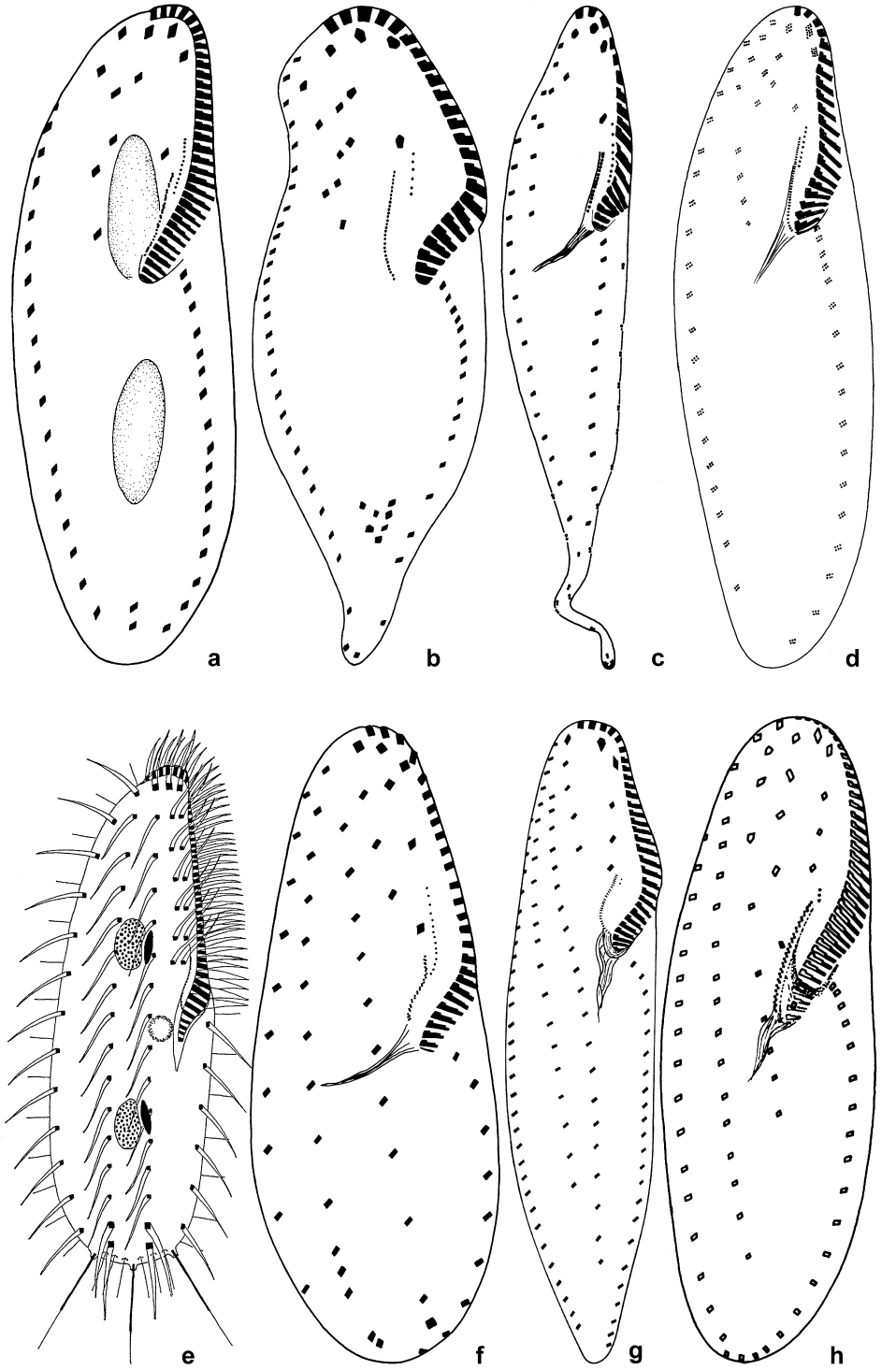
8 (5) Body large (about 200–350 × 70–150 µm in life); distinct transverse cirri present (Fig. 9h). . . . . *Saudithrix* (p. 647)
- No such combination of features. **9**

9 Body length:width ratio about 10–20:1; adoral zone usually occupying 16% or less of body length (e.g., Fig. 8d, g, 9b, f). **10**
- No such combination of features. **11**

Fig. 7a–h Ventral infraciliature of representatives of gonostomatid genera (sources of illustrations see individual descriptions; the features refer to the genus). **a, b:** *Gonostomum affine* and *G. namibiense*; transverse cirri present. **c, d:** *Paragonostomum caudatum* and *P. simplex*; transverse cirri lacking. **e, f:** *Wallackia schiffmanni* and *W. bujoreani*; caudal cirri long and prominent. **g:** *Cladotricha australis*; two long frontoventral rows, highly saline habitat. **h:** *Neowallackia franzi*; caudal cirri lacking. →

[1] If you cannot identify your specimen/population using this lead and the subsequent couplets, use the option "Non-saline habitats".

[2] Note that *Urosoma* is, like *Hemiurosoma* Foissner et al., 2002a (for review, see Berger 2008, p. 614), very likely a non-oxytrichid Dorsomarginalia according to a recent hypothesis (Berger 2008, p. 46).



Legend on p. 46

10 One left and one right marginal row (Fig. 9b, f). **17**
- Two left and two right marginal rows (at least outer rows composed of widely spaced cirri; Fig. 8d, g). **16**

11 (9) One long frontoventral row (Fig. 9g). . . . . *Orthoamphisiella* (p. 620)
- Two or more frontoventral rows (e.g., Fig. 8c, f, 9d). **12**

12 Caudal cirri lacking (e.g., Fig. 9d). . . . . *Deviata* (p. 555)
- Caudal cirri present, difficult to recognise in *Neogeneia* (e.g., Fig. 8c, e, 84c). **13**

13 Dorsomarginal kinety not clearly separated from right marginal row (Fig. 84c). . . . . *Neogeneia* (p. 481)
- Dorsomarginal kinety clearly separated from right marginal row present (e.g., Fig. 73e). **14**

14 Transverse cirri (inconspicuous!) present (Fig. 8e). . . . . *Fragmocirrus* (p. 455)
- Transverse cirri lacking (Fig. 8b, c). **15**

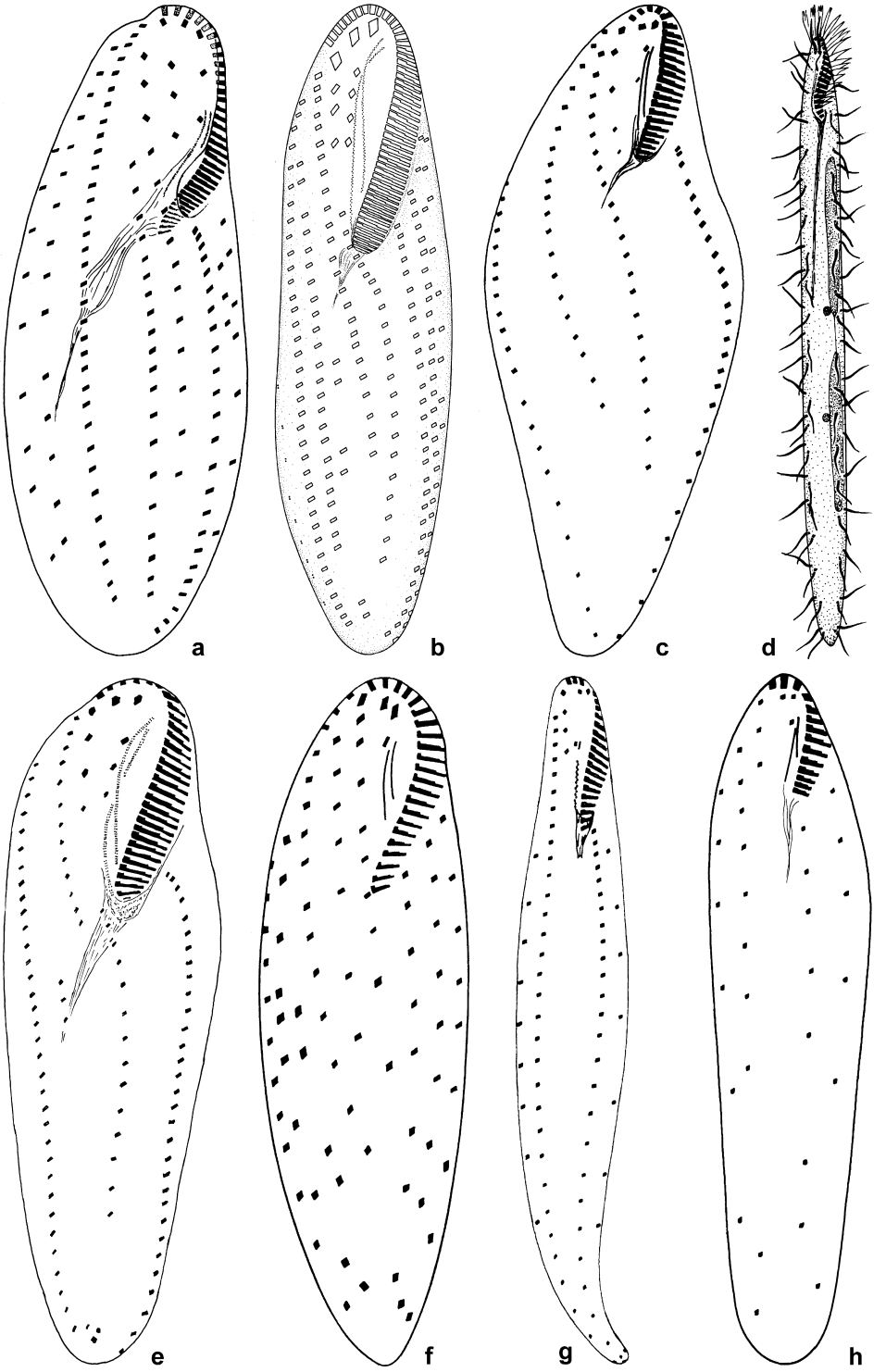
15 In total five dorsal kineties (dorsomarginal kinety and parental rows included; Fig. 8b, 73e). . . . . *Parakahliella* (p. 397)
- In total four dorsal kineties (Fig. 8c, 76i). . . . . *Afrokahliella* (p. 432)

16 (10) All rows with widely spaced cirri (Fig. 8d, h). . . . . *Perisincirra* (p. 463)
- Only outermost rows with widely spaced cirri (Fig. 8g). *Engelmanniella* (p. 498)

17 (10) Saline to highly saline habitat (Fig. 9f). . . . . *Apourosomoida* (p. 684)
- Non-saline habitat (Fig. 9b). . . . . *Circinella* (p. 309)

Fig. 8a–h Ventral infraciliature of representatives of kahliellid genera (sources of illustrations see individual descriptions; the features refer to the genus). **a:** *Kahliella simplex*; gonostomoid oral apparatus, parental rows with widely spaced cirri. **b:** *Parakahliella macrostoma*; in total five dorsal kineties. **c:** *Afrokahliella namibicola*; in total four dorsal kineties. **d, h:** *Perisincirra kahli* and *P. paucicirrata*; all rows with widely spaced cirri. **e:** *Fragmocirrus espeletiae*; transverse cirri present, but indistinct. **f:** *Neogeneia hortualis*; many cirral rows, (distinct) dorsomarginal kinety lacking. **g:** *Engelmanniella mobilis*; slender, outer marginal rows with widely spaced cirri. →

Fig. 9a–h Ventral infraciliature of representatives of gonostomatid genera (incertae sedis; a, b) and genera of uncertain systematic position (c–h). For sources of illustrations see individual descriptions; the features refer to the genera. **a:** *Trachelochaeta bryophila*; anterior body portion narrowed, long caudal cirri. **b:** *Circinella arenicola*; very slender, adoral zone very short. **c:** *Pseudokahliella marina*; many cirral rows, marine. **d:** *Deviata abbrevescens*; transverse and caudal cirri lacking, one, two, or three dorsal kineties. **e:** *Stenotricha arenicola*; marine, cephalised, distinct transverse cirri, short row of postoral ventral cirri. **f:** *Apourosomoida elongata*; highly saline habitat, slender, adoral zone with gap. **g:** *Orthoamphisiella stramenticola*; more than one buccal cirrus, one long frontoventral row, transverse and caudal cirri lacking. **h:** *Saudithrix terricola*; very large, many cirral rows, transverse cirri present. Figures on page 50. ⇉



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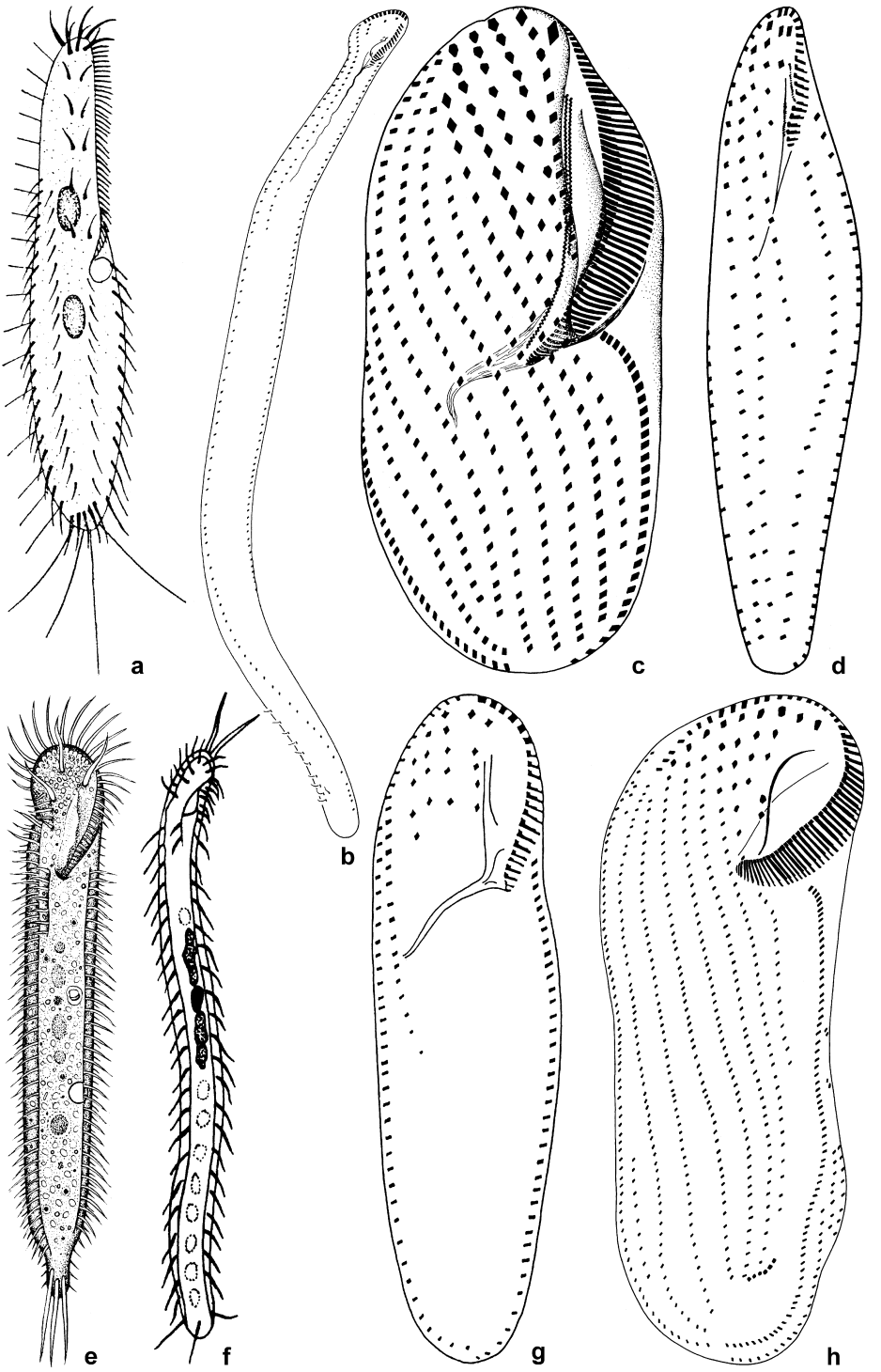

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Gonostomatidae Small & Lynn, 1985

1985 **Gonostomatidae n. fam.**[1] – Small & Lynn, Phylum Ciliophora, p. 455 (original description; Table 3). Name-bearing type genus: *Gonostomum* Sterki, 1878.

1985 **Cladotrichidae n. fam.**[2] – Small & Lynn, Phylum Ciliophora, p. 456 (original description; Table 4). Name-bearing type genus: *Cladotricha* Gaievskaïa, 1925.

1986 **Gonostomidae (n. fam.)** – Culberson, Diss. Abstr. int., 46B: 2589 (original description). Name-bearing type genus: *Gonostomum* Sterki, 1878.

2001 **Gonostomatidae Small and Lynn, 1985** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 107 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2001 **Gonostomidae Culberson, 1986** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 108 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: Goode & Bean (1895, p. 97) defined the fish family Gonostomidae based on *Gonostoma* Rafinesque, 1810[3]. Later, the spelling changed to Gonostomatidae (e.g., Kalabis & Schultz 1974, p. 184; Lancraft et al. 1988). However, the original spelling (Gonostomidae) of the fish family is also still in general use (e.g., Bowmaker & Wagner 2004, p. 2379). The ciliate family based on *Gonostomum* Sterki, 1878 was established twice, namely by Small & Lynn (1985) as Gonostomatidae, and by Culberson (1986) as Gonostomidae. Both ciliate names are therefore homonyms of the fish family. The final adjustment of this rather tricky situation needs the collaboration with a linguist, a specialist dealing with this fish-group who knows all about the nomenclature of this taxon, and the International Commission on Zoological Nomenclature (ICZN 1999, Article 55.3.1). Preliminary I suggest to use the original spelling of the fish family (Gonostomidae Goode & Bean, 1895) and the older version of the ciliate family (Gonostomatidae Small & Lynn, 1985). This simple solution prevents homonymy.

As mentioned above, the family Gonostomatidae Small & Lynn, 1985 is based on *Gonostomum* Sterki, 1878, with *Oxytricha affinis* Stein, 1859 as type species (Berger 1999, 2001). Interestingly, Small & Lynn (1985, p. 461, their Fig. 44A) did not allocate *O. affinis* to *Gonostomum*, but to *Trachelostyla* Borror, 1972, which they used as nominotypical genus of a further new family, the Trachelostylidae Small & Lynn, 1985 (for review, see Berger 2008, p. 471). This approach caused a rather tricky situation, which is nomenclaturally not possibly because a genus is defined via the type species, that is, one cannot accept a genus, but simultaneously include its type species in another genus (ICZN 1999). In the second edition of the "Illustrated guide", Lynn & Small (2002) synonymised the Gonostomatidae with the Trachelostylidae, but the misclassification of *G. affine* in *Trachelostyla* was retained (further details, see remarks).

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[1] Small & Lynn (1985) provided the following diagnosis: With 2 or more frontoventral cirral files parallel to long axis of oral region along its right border; at least 2 frontoventral files extend almost length of body.

[2] Small & Lynn (1985) provided the following diagnosis: Frontal file, on right, rarely extends past midbody; at least 1 left and 1 right marginal files.

[3] Paper not mentioned in reference section.

Characterisation (A= supposed apomorphy): Non-dorsomarginalian Hypotricha. Oral apparatus gonostomatid (A). More or less strongly modified 18-frontal-ventral-transverse cirri pattern, that is, taxa with roughly 18 frontal-ventral-transverse cirri, but also with distinct rows due to strongly increased number of cirri per anlage included. Usually one left and one right marginal row. Mostly three bipolar dorsal kineties with each one caudal cirrus. Dorsomarginal kineties and kinety fragmentation lacking.

The ground pattern of the Gonostomatidae: Below the supposed ground pattern of the Gonostomatidae is briefly discussed (see also remarks). For a brief explanation of the term ground pattern, see chapter 2.2 of the general section of Berger (2008, p. 23).

Apomorphy of the Gonostomatidae: This group has – at the present state of knowledge – only one morphological apomorphy, namely, the striking "gonostomatid" oral apparatus (e.g., Fig. 3a, 24a–d; Fig. 20c, 21d in Berger 1999). The adoral zone is not shaped like a question mark as in most other hypotrichs (e.g., Fig. 6a in Berger 1999), but the middle portion is straight and extends along the left body margin, causing the proximal portion to become abruptly bent (knee-shaped; see etymology of genus-group name) towards the centre of the cell (Berger & Foissner 1997, Berger 1999). The paroral consist of (commonly) few, usually widely spaced cilia and extends beyond the anterior end of the endoral, which is more or less of ordinary structure (Fig. 24d). The buccal cavity is very small and flat. For a general description of the oral apparatus of the hypotrichs, see Berger (1999) and Foissner & AL-Rasheid (2006). Perhaps the gonostomatids have further apomorphies, for example, morphogenetic ones. But at present, too few detailed data are available. In addition, I cannot exclude that one or two genera included are intrinsically no gonostomatid.

The plesiomorphies of the gonostomatids (e.g., two marginal rows, caudal cirri present, three bipolar dorsal kineties) are the same as for the Hypotricha. Thus, refer to chapter 2.2 of the general section of Berger (2008).

Remarks: Previously I classified *Gonostomum*, whose type species *Oxytricha affinis* has a slightly modified 18-cirri pattern[1], in the Oxytrichinae because we supposed that the 18-cirri pattern is an apomorphy of the oxytrichids (Berger & Foissner 1997, Berger 1999). Therefore we had to assume that the simple dorsal kinety pattern of *Gonostomum* – three bipolar kineties with one caudal cirrus each (Fig. 15b) – evolved from the much more complex *Oxytricha* pattern (Fig. 24a in Berger 1999) via a loss of the kinety fragmentation (*Urosomoida* pattern; Fig. 24b in Berger 1999) and a further loss of the dorsomarginal kinety (*Gonostomum* pattern; Berger 1999, p. 73). Consequently, the Gonostomatidae became a junior synonym (or subgroup) of the oxytrichids in the first volume of the revision. However, a re-evaluation of the morphological and morphogenetic data and the broader molecular analyses available since then strongly indicate that the 18-cirri pattern is not an apomorphy of the oxytrichids, but of the Hypotricha, that is, this pattern likely evolved in the last

[1] Some left transverse cirri and pretransverse ventral cirri are usually lacking and the "postoral" ventral cirri are right of the adoral zone (cp. Fig. 2a with Fig. 3a).

common ancestor of the hypotrichs and is therefore part of the ground pattern of the whole group (Fig. 2a; Fig. 6a [square 9], 9a [square 1] in Berger 2008; Berger 2007, 2008a, Schmidt et al. 2007). Thus, I preliminary eliminated the non-monophyletic group Oxytrichinae which is – according to morphological and ontogenetic data (e.g., presence [*Oxytricha granulifera*] or lack [*Oxytricha lanceolata*] of dorsal kinety fragmentation; for review see Berger 1999) and molecular analyses – an artificial assemblage of flexible 18-cirri hypotrichs (Berger 2008, p. 47). Supposed that the hypothesis about the early origin of the 18-cirri pattern is correct, this pattern is the beginning of the various cirral patterns so far described for hypotrichs.

Morphological and morphogenetic features which indicate a misplacement of *Gonostomum* in the oxytrichids and the Dorsomarginalia, respectively, are the lack of the oxytrichid dorsal kinety fragmentation and the lack of a dorsomarginal kinety.

The molecular analyses differ rather distinctly from each other as concerns, inter alia, the position of *Gonostomum* so that we must be somewhat suspicious of these data and should not over-interpret details. Recent analyses comprising a considerable number of species show that *Gonostomum* basically clusters outside the Dorsomarginalia, that is, at or near the base of the Hypotricha tree, at least usually outside the typical oxytrichids and often close to amphisiellids, and/or *Trachelostyla*, and/or urostyloids (e.g., Affa'a et al. 2004, Agatha et al. 2004, 2005, Kim et al. 2005, Shin 2005, Gong et al. 2007, Schmidt et al. 2007, Shao et al. 2007, 2008, Foissner & Stoeck 2008, Paiva et al. 2009, Yi et al. 2009). Amphisiellids and urostyloids lack, like *Gonostomum*, a dorsomarginal kinety and kinety fragmentation (Berger 2006a, 2008). *Trachelostyla* also lacks a dorsomarginal kinety and has an adoral zone which is reminiscent of that of *Gonostomum*, but has a special type of kinety fragmentation (Shao et al. 2007; for review, see Berger 2008). A position of *Gonostomum* outside the Dorsomarginalia is also indicated by the resting cyst, a feature usually underrepresented in ciliate taxonomy (Foissner et al. 2008). The cyst of *G. affine* has the same ultrastructure as the cysts of the urostyloids *Urostyla grandis*, *Anteholosticha adami*, and *Pseudourostyla levis* (Matsusaka et al. 1989, p. 136). The *Urostyla*-type cyst has, according to Matsusaka et al. (1989), a two-layered cyst wall, a granular layer, and contains cortical microtubules and basal bodies, but not ciliary shafts. By contrast, the *Oxytricha*-type cyst has a three-layered cyst wall, a granular layer, and contains no microtubular organelles, with some exceptions containing only cytoplasmic microtubules.

All these findings and data (18-cirri pattern is not an apomorphy of the oxytrichids; dorsomarginal kinety and kinety fragmentation lacking; cyst of *Urostyla*-type; basal branching in molecular trees[1]) strongly support the classification of *Gonostomum* outside the Dorsomarginalia and therefore the reactivation[2] of the Gonosto-

[1] For a more detailed discussion of the various positions of *Gonostomum* in molecular trees, see *G. strenuum*.

[2] Just recently, Foissner & Stoeck submitted a paper to the European Journal of Protistology (2010) where they described a highly interesting gonostomatid hypotrich from a bromelian and also reactivated the Gonostomatidae. Since a reactivation is basically a taxonomic process, no nomenclatural problems arise when a taxon is two-times reactivated.

matidae Small & Lynn, 1985 (Table 3). Originally, the Gonostomatidae comprised the genera *Trachelochaeta* Šrámek-Hušek, 1954 (p. 300), *Wallackia* Foissner, 1976 (p. 206), and *Gonostomum* (p. 58), however, without the type species *G. affine*, as already mentioned above (Small & Lynn 1985). Culberson (1986) did not assign genera to the "Gonostomidae", one of three families (Oxytrichidae, Amphisiellidae) of the "suborder Oxytrichina". By contrast, Lynn & Small (2002) submerged the Gonostomatidae in the Trachelostylidae Small & Lynn, 1985 and listed five representative genera, namely, *Terricirra* Berger & Foissner, 1989a, *Hemisincirra* Hemberger, 1985, *Trachelostyla* Borror, 1972, *Lamtostyla* Buitkamp, 1977a, and *Gonostomum*, again with the type species *G. affine* in *Trachelostyla*. Recently, Lynn (2008) again put the gonostomatids into the synonymy of the Trachelostylidae and included *Cossothigma* Jankowski, 1978, *Gonostomum*, *Hemisincirra*, *Paragonostomum* Foissner et al., 2002, *Spirotrachelostyla* Gong et al., 2006, *Terricirra*, and *Trachelostyla*. By contrast, I consider both the Gonostomatidae and the Trachelostylidae as valid taxa. The trachelostylids have been revised just recently in the third volume of the monograph, comprising only *Trachelostyla* (name-bearing type) and *Spirotrachelostyla* (Berger 2008, p. 471). *Cossothigma*, *Hemisincirra*, *Lamtostyla*, and *Terricirra* were assigned to the amphisiellids (Berger 2008), whereas *Gonostomum*, *Paragonostomum*, *Wallackia*, and some other genera are classified in the Gonostomatidae revised in the present volume.

A close relationship of the gonostomatids and the trachelostylids is indicated by the following features (see also Berger 2008, p. 477): (i) the gonostomatid oral apparatus, especially the laterally running adoral zone; (ii) the position of the so-called postoral ventral cirri right of the proximal part of the adoral zone; and (iii) a basal branch-off of both taxa in some molecular trees (Gong et al. 2006, Shao et al. 2007, Yi et al. 2009). However, the rather diverging results of the phylogenetic analyses based on 18S rDNA show that these data must not be overinterpreted.

Cladotricha is now also assigned to the Gonostomatidae. Thus, the Cladotrichidae Small & Lynn, 1985 become a junior synonym of the gonostomatids. Further studies will show whether or not this group can be used again, for example, as subgroup of the Gonostomatidae. Some other workers (e.g., Tuffrau & Fleury 1994, Lynn & Small 2002, Jankowski 2007, Lynn 2008) synonymised the Cladotrichidae with the Kahliellidae (Tables 7, 10–12).

The most striking feature of the Gonostomatidae is the "gonostomatid" oral apparatus (see ground pattern above). The question is whether or not these conspicuous details of the oral apparatus are evolutionary novelties of the gonostomatids. If so, then we have to postulate that a similar oral apparatus evolved convergently in at least two dorsomarginalian taxa, namely, *Kahliella* (p. 347) and *Urosoma* Kowalewskiego, 1882 (Berger 1999, p. 396; note that *Urosoma* is very likely not an oxytrichid, as supposed by Berger 1999, but a non-oxytrichid dorsomarginalian, because it lacks dorsal kinety fragmentation; Berger 2008, p. 46). However, when the similarity is based on a common origin, then we would have to assume that the gonosto-

matid oral apparatus is a rather old feature possibly already occurring in the last common ancestor of the hypotrichs.

Unfortunately, only very few details are known about the undulating membranes of the trachelostylids. According to Gong et al. (2006), the endoral of *Trachelostyla pediculiformis* is about half as long (6 µm) as the paroral (13 µm; Fig. 96f in Berger 2008). In addition, both membranes obviously have more or less the same, ordinary structure, that is, they are composed of narrowly spaced cilia. By contrast, the paroral of the gonostomatids (e.g., *Gonostomum*, *Paragonostomum*) is made up of a low to very low number of widely spaced cilia (e.g., Fig. 7a–h). *Diophrys* and discocephalids, two spirotrichs with two undulating membranes (very likely) branching off outside the Perilemmaphora (oligotrichs + hypotrichs; Berger 2008, p. 25; Shao et al. 2008), have more or less ordinary undulating membranes, indicating that the special paroral of the gonostomatids is a novelty for this group.

As mentioned above, a further interesting feature of the core-gonostomatids (*Gonostomum*, *Paragonostomum*) are the anteriorly displaced "postoral" ventral cirri (e.g., Fig. 3a). When *Gonostomum* was classified in the oxytrichids, we had to postulate that this displacement is an apomorphy for *Gonostomum* (Berger & Foissner 1997, Berger 1999, p. 66). Recently, I discussed that this "deviating" position right of the posterior portion of the adoral zone could be part of the ground pattern of the Hypotricha because euplotids, which branch off at/near the base of the (molecular) Spirotricha tree, have a far posteriorly extending adoral zone so that most/all frontoventral cirri are right of the adoral zone (Berger 2008, p. 48). Thus, the "deviating" position of the postoral ventral cirri in *Gonostomum* and *Trachelostyla* is perhaps a remain taken over from the early spirotrichs (Berger 2008, p. 27). If this assumption is correct, then the postoral position of the postoral ventral cirri would be an apomorphy for the remaining hypotrichs.

The dorsal kinety pattern of the gonostomatids – three bipolar kineties each bearing a caudal cirrus (e.g., Fig. 23e) – corresponds that of the ground pattern of the hypotrichs (Fig. 2a). *Neowallackia* likely has lost the caudal cirri (Fig. 52e, 53b). By contrast, *Trachelostyla pediculiformis*, type of *Trachelostyla* and the trachelostylids, has a very curious pattern of dorsal kinety formation (Shao et al. 2007; for review, see Berger 2008, p. 687). This species has usually six more or less bipolar kineties, but only two of them (kinety 1 and 6) are ontogenetically active. *Spirotrachelostyla tani*, the second trachelostylid species described in detail, has invariably only two dorsal kineties, which very likely originate in the ordinary way, that is, by intrakinetal proliferation at two levels. Supposed that *Spirotrachelostyla* is indeed closely related to *Trachelostyla*, the curious pattern described for *T. pediculiformis* is obviously only an apomorphy of *Trachelostyla*, or even only of *T. pediculiformis*.

The adoral zone of *Parastrongylidium* Fleury & Fryd-Versavel, 1984 is somewhat reminiscent of that of *Gonostomum* (Fleury & Fryd-Versavel 1984, Aescht & Foissner 1992, Salvadó & Fernández-Galiano 1997, Siqueira-Castro et al. 2009). However, the other elements of the infraciliature do not literally support an inclusion in the Gonostomatidae, although it cannot be excluded that this small group is in-

deed a member of the gonostomatids. An inclusion in the Kahliellidae seems not appropriate because a dorsomarginal kinety is lacking. According to Aescht & Foissner (1992), Tuffrau & Fleury (1994, p. 137), and Lynn (2008, p. 359) *Parastrongylidium* belongs to the strongylidiids/spirofilids. Thus, this genus will be treated in a later volume of the treatise.

The characterisations of the genera are partly rather vague because important data are lacking or the species assigned to a certain genus are rather different in the features usually used at genus level. Further data will perhaps demonstrate that not all genera at present assigned to the gonostomatids are in fact closely related.

Genera included in the Gonostomatidae: *Gonostomum* Sterki, 1878 (type genus); *Paragonostomum* Foissner, Agatha & Berger, 2002; *Wallackia* Foissner, 1976; *Cladotricha* Gaievskaïa, 1925; *Neowallackia* gen. nov. Incertae sedis: *Trachelochaeta* Šrámek-Hušek, 1954; *Circinella* Foissner, 1994.

Gonostomum is the name-bearing type genus of the Gonostomatidae and therefore its inclusion in this groups needs no explanation.

Paragonostomum was established only recently by Foissner et al. (2002a). It differs from *Gonostomum* mainly by the lack of transverse cirri and the often more or less distinctly tailed body end (p. 172). By contrast, the rear body portion is usually rounded in *Gonostomum*, except for *G. namibiense*, which is also tailed.

Wallackia is reminiscent of *Gonostomum* and *Kahliella* as concerns the gonostomatid adoral zone. Since a dorsomarginal kinety is lacking, a classification in the Dorsomarginalia, to which the kahliellids belong, seems not plausible. Further, in *Wallackia* no parts of the parental ciliature are retained after division, a feature often occurring in the kahliellids. Thus, I follow Small & Lynn (1985), who originally included *Wallackia* in the Gonostomatidae.

Cladotricha is a difficult genus because the type species is not known in detail. Accurately described "*Cladotricha*" species have a gonostomatid oral apparatus and dorsal kinety pattern (three bipolar kineties with caudal cirri) so that an assignment to the gonostomatids seems to be the best solution at the present state of knowledge. Furthermore, *Cladotricha* is obviously very similar to *Wallackia* which differ mainly in the shape of the caudal cirri (normal vs. shaped like a Pasteur pipette) and the habitat, that is, saline to hyper-saline waters (e.g., salt lake, brine) against non-saline to saline soils. Only a detailed reinvestigation of *C. koltzowii*, type of the genus, will clear up the somewhat unsatisfying situation.

Neowallackia is a new genus with *Gonostomum franzi* Foissner, 1982 as type species (p. 280). This only lately discovered species has a rather turbulent history (within 27 years it was assigned to three genera, namely, *Gonostomum*, *Kahliella*, and *Orthoamphisiella*), which should be stabilised by the assignment to an own genus. A major difference to *Wallackia* is the lack of caudal cirri, organelles which are very conspicuous in *Wallackia*. Recently, Alekperov (2005) described a *Trachelochaeta* species which can be easily classified in *Neowallackia*.

Trachelochaeta is a little known genus comprising only the type species in the present monograph. Some important details (e.g., morphogenesis of cirral pattern,

dorsal kinety pattern) are not known making a reliable classification impossible. The gonostomatid oral apparatus and the *Wallackia*-like cirral pattern indicate a relationship with the gonostomatids. Thus, *Trachelochaeta bryophila* is preliminarily classified as incertae sedis in the Gonostomatidae (further details, see genus section).

Circinella comprises three very slender soil species which have a very small oral apparatus (about 6–8% of body length). Its assignment to the gonostomatids is only tentatively.

Key to the genera of the Gonostomatidae and to similar taxa

The separation of the genera included in the Gonostomatidae is rather difficult, indicating that they are closely related. Protargol impregnation should be made to know the cirral pattern exactly (e.g., presence/absence of transverse and/or caudal cirri). Recently, Foissner & Stoeck (2010; European Journal of Protistology, in press) discovered *Cotterillia bromelicola*[1] in Mexican bromelians. It has a dorsal side covered with bipolar bristles rows and combined rows (anterior portion with dorsal bristles, rear portion with cirri); further details on this highly interesting species, see original description.

1 Body worm-shaped, that is, very slender; adoral zone occupies only about 6–8% of body length (Fig. 57a, 60a, 61a). . . . . *Circinella* (p. 309)
- Body and adoral zone not as above. **2**
2 Transverse cirri present (e.g., Fig. 3a, 10b, 22a, e, 56a). **3**
- Transverse cirri lacking (e.g., Fig. 30a, h, 48a, g). **4**
3 Anterior body portion narrowed; five transverse cirri; two long frontoventral rows; caudal cirri very long (Fig. 56a–c). . . . . *Trachelochaeta* (p. 300)
- Anterior body portion not narrowed; less than five transverse cirri; non or one long frontoventral row; caudal cirri about of same length as marginal cirri (e.g., Fig. 10b, 22a–j, 25a–f, 26a). . . . . *Gonostomum* (p. 58)
4 (2) Caudal cirri shaped like a Pasteur pipette (Fig. 39a, d, 42l). . . . . *Wallackia* (p. 206)
- Caudal cirri not as above or lacking. **5**
5 Caudal cirri lacking (e.g., Fig. 52a–e). . . . . *Neowallackia* (p. 280)
- Caudal cirri present (e.g., Fig. 30a, 35a, 43a–m, 48a–f). **6**
6 Saline to hyper-saline habitat (e.g., salt lake, brine). . . . . *Cladotricha* (p. 235)
- Non-saline soil. . . . . *Paragonostomum* (p. 172)

[1] The name *Cotterillia bromelicola* is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3).

Gonostomum Sterki, 1878

1878 ***Gonostomum* nov. gen.**[1] – Sterki, Z. wiss. Zool., 31: 36, 57 (original description). Type species (by original designation; see nomenclature): *Oxytricha affinis* Stein, 1859.

1882 ***Plagiotricha*, S.K.** – Kent, Manual Infusoria II, p. 771 (original description of synonym). Type species (by original designation): *Oxytricha strenua* Engelmann, 1862.

1886 ***Gonostomum* Sterki** – Blochmann, Thierwelt des Süsswassers, p. 77 (guide).

1888 ***Stichochaeta*, non Clap. et Lachm.** – Gourret & Roeser, Archs Biol., 8: 186, 187, pro parte (taxonomy of protozoa from Corsica; see remarks).

1889 ***Gonostomum* Sterki 1878** – Bütschli, Protozoa, p. 1748 (revision of ciliates).

1895 ***Gonostomum* Sterki** – Blochmann, Thierwelt des Süsswassers, p. 113 (guide).

1926 ***Gonostomum* Sterki** – Lepsi, Infusorien des Süsswassers und des Meeres, p. 82 (guide to ciliates).

1932 ***Gonostomum* Sterki, 1878** [2] – Kahl, Tierwelt Dtl., 25: 597 (detailed revision).

1936 ***Gonostomum* Sterki, 1878** – Bhatia, Protozoa: Ciliophora, p. 372 (guide to protozoa of British India).

1950 ***Gonostomum* Sterki** – Kudo, Protozoology, p. 670 (textbook on protozoology).

1961 ***Gonostomum* Sterki** – Corliss, Ciliated Protozoa, p. 170 (revision of ciliate families).

1972 ***Gonostomum* Sterki, 1878** – Borror, J. Protozool., 19: 14 (generic revision of hypotrich).

1974 ***Gonostomum* Sterki** – Stiller, Fauna Hung., 115: 88 (revision of Hungarian hypotrichs).

1979 ***Gonostomum* Sterki, 1878** – Jankowski, Trudy zool. Inst., 86: 55 (generic catalogue of hypotrichs; see nomenclature).

1979 ***Plagiotricha* Kent, 1882** – Jankowski, Trudy zool. Inst., 86: 62 (generic catalogue of hypotrichs; see nomenclature).

1979 ***Gonostomum* Sterki, 1878** – Corliss, Ciliated Protozoa, p. 309 (revision of ciliates).

1979 ***Gonostomum* Sterki, 1878** – Tuffrau, Trans. Am. microsc. Soc., 98: 526 (revision of hypotrichs).

1982 ***Gonostomum* Sterki, 1878** – Foissner, Arch. Protistenk., 126: 74 (brief note on systematics).

1982 ***Gonostomum* Sterki, 1878**[3] – Hemberger, Dissertation, p. 190 (detailed revision of hypotrichs).

1983 ***Gonostomum* Sterki, 1878** – Curds, Gates & Roberts, British and other freshwater ciliated protozoa, p. 406 (generic revision of ciliates; see remarks).

1984 ***Gonostomum* Sterki, 1878** – Maeda & Carey, Bull. Br. Mus. nat. Hist. (Zool.), 47: 8 (detailed revision of *Trachelostyla* and *Gonostomum*).

1985 ***Gonostomum*** [4] – Small & Lynn, Phylum Ciliophora, p. 455 (guide to ciliate genera; see remarks).

1986 ***Gonostomum* Sterki, 1878** – Dragesco & Dragesco-Kernéis, Faune tropicale, 26: 453 (guide to ciliates of Africa).

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[1] Sterki (1878, p. 57) provided the following characterisation and explanation (for English translation, see nomenclature): Ferner ist von *Oxytricha* abzutrennen *O. affinis* St., die ich eingehend zu untersuchen Gelegenheit hatte. Ausserdem fanden sich hier 2 oder 3 neue Arten, die ganz nach demselben Typus gebaut sind; ich vereinige sie zur Gattung *Gonostomum* n. gen., die wesentlich durch die Lage und Form des Peristoms und die dadurch bedingte Configuration des Stirnfeldes, sowie durch die Bewimperung characterisiert ist, und eine sehr einheitliche wohlumgrenzte Gruppe bildet, zu der offenbar auch *O. strenua* Engelmann zu ziehen ist.

[2] Kahl (1932) provided the following characterisation: Körper biegsam, Frontalcirren 8 oder mehr. 1 oder 2 Ventralreihen schräg, verkürzt. Transversalcirren 4 oder 5. 2 Marginalreihen. Ein ergänzendes Merkmal ist die an die linke Seitenwand verschobene adorale Zone, die erst kurz vor dem Munde auf die Ventralfläche schwenkt.

[3] Hemberger (1982) provided the following diagnosis: Je 1 rechte und linke Marginalreihe; nur 2 unscheinbare Ventralcirren vor den Transversalcirren; AMZ lange an der linken Körperseite verlaufend; 3 Caudalcirren; Cirrenentwicklung aus 5 FVT-Anlagen; diese entwickeln sich alle auf dem Frontalfeld des Ausgangstieres; große Variabilität in Cirrenzahl und -anordnung.

[4] Small & Lynn (1985) provided the following characterisation: Cirral files not extended backward as far as transverse cirri.

1987 ***Gonostomum* Sterki, 1878** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (revision of hypotrich orders).
1994 ***Gonostomum* Sterki, 1878** – Tuffrau & Fleury, Traite de Zoologie, 2: 143 (revision of hypotrich families).
1994 ***Gonostomum* Sterki, 1878** – Shin, Dissertation, p. 105 (systematics of Korean hypotrichs).
1997 ***Gonostomum* Sterki, 1878** – Berger & Foissner, Arch. Protistenk., 148: 145 (phylogenetic analyses and generic revision of oxytrichids; for characterisation, see Berger 1999).
1999 ***Gonostomum* Sterki, 1878** [1] – Berger, Monographiae biol., 78: 367 (detailed revision).
1999 ***Gonostomum* Sterki, 1878** – Shi, Acta Zootax. sinica, 24: 259 (generic revision of hypotrichs).
1999 ***Gonostomum* Sterki, 1878** – Shi, Song & Shi, Progress in Protozoology, p. 108 (generic revision of hypotrichs).
2001 ***Gonostomum* Sterki 1878** – Aescht, Denisia, 1: 76 (catalogue of generic names of ciliates).
2001 ***Gonostomum* Sterki, 1878** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 29 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Gonostomum* Sterki, 1878** [2] – Lynn & Small, Phylum Ciliophora, p. 459 (guide to ciliate genera).
2007 ***Gonostomum* Sterki, 1878** – Jankowski, Phylum Ciliophora, p. 464 (generic revision of ciliates).
2007 ***Plagiotricha* Kent, 1882** – Jankowski, Phylum Ciliophora, p. 464 (generic revision of ciliates).
2008 ***Gonostomum* Sterki, 1878** – Lynn, Ciliated protozoa, p. 361 (revision of ciliate families).

Nomenclature: A derivation of the genus-group name *Gonostomum* was provided neither in the original description, the review by Berger (1999), nor in any other paper. *Gonostomum* is a composite of the Greek substantive *he gonía* (knee, corner, angle), the thematic vowel *·o-*, the Greek substantive *to stóma* (mouth, opening; Hentschel & Wagner 1996, p. 278, 559), and the suffix *-um*. It obviously refers to the angled (knee-shaped) adoral zone of membranelles. Neuter gender (Aescht 2001, p. 284). *Gonostomum* Sterki, 1878 is the name-bearing type genus of the Gonostomatidae Small & Lynn, 1985 and Gonostomidae Culberson, 1986, but not of the Gonostomidae Goode & Bean, 1895 which is based on the fish genus *Gonostoma* Rafinesque, 1810[3]. *Plagiotricha* is a composite of the Greek adjective *plagios* (oblique) and the Greek noun *trichos* (hair; cirrus in present case) (Kent 1882). Likely, it refers to the "one or more oblique rows of ventral setae".

The type fixation in *Gonostomum* is somewhat cryptic at the first glance and caused some authors (Borror 1972, Jankowski 1979) to assume that *Oxytricha strenua* Engelmann, 1862 is the type species of *Gonostomum*. However, this is incorrect and because the paper by Sterki (1878) is in German I explain the situation in detail. Sterki (1878, p. 36) included in *Gonostomum* "*Oxytricha affinis* Stein, *Oxytricha strenua* Engelmann and two or three new species", that is, at this site of the paper he did not fix a type. In the appendix, Sterki (1878, p. 57, point 6) defined *Gonostomum* as follows (see footnote 1 on p. 58 for original German version): "Further,

[1] Berger (1999) provided the following characterisation (based on Berger & Foissner 1997): Adoral zone of membranelles and undulating membranes in *Gonostomum* pattern. Frontoventral cirri roughly in V-shaped pattern. Postoral ventral cirri right of adoral zone. Usually fewer than 4 transverse cirri. One right and 1 left row of marginal cirri. Three dorsal kineties. Caudal cirri present. Primary primordia. Dorsal morphogenesis in *Gonostomum* pattern.

[2] Lynn & Small (2002) provided the following characterisation: Paroral and endoral parallel to each other with endoral anterior to paroral; some frontoventral cirri form a file along anterior right border of peristomal area; transverse cirri; caudal cirri, posterior and dorsal.

[3] Paper not mentioned in reference section.

Oxytricha affinis, which I could study in detail, has to be separated from *Oxytricha*. In addition, two or three new species were found which have to be assigned to this type; I unify them in the genus *Gonostomum* n. gen., which is mainly characterised by the position and shape of the peristome and the resulting configuration of the frontal field as well as by the ciliature, and which forms a homogenous, well bounded group, to which obviously *O. strenua* Engelmann has to be assigned too." From the first sentence it is clear that *O. affinis* is the type species, and not *O. strenua*, which apparently also belongs to *Gonostomum*. The two or three new species mentioned by Sterki have never been described. Jankowski (1979) incorrectly mentioned *O. affinis* as type species of *Plagiotricha* Kent, 1882. For further notes on *Plagiotricha* Kent, 1882, see Berger (1999, p. 368) and remarks.

Characterisation (A = supposed apomorphy): Gonostomatidae with six (I–VI) frontal-ventral-transverse cirri anlagen and reduced 18-cirri pattern (reduction usually concerns left transverse cirri) or increased number of cirri mainly formed by anlagen V and VI. Postoral ventral cirri right of proximal portion of adoral zone, in *G. strenuum* partially extending onto postoral area. Pretransverse ventral and transverse cirri present. Three bipolar dorsal kineties, that is, dorsomarginal kineties and kinety fragmentation lacking; each kinety bearing a caudal cirrus. Anlagen II–VI of proter and opisthe originate from primary primordia. Mainly terrestrial, sometimes limnetic.

Additional characters: Body mainly small (usually below 100 µm long), distinctly higher values (up to 200 µm) described for *G. gonostomoidum* have to be confirmed; flattened dorsoventrally about 2:1; flexible. Contractile vacuole about at level of buccal vertex, near left body margin or slightly to distinctly displaced inwards. Cortical granules present, usually rood-shaped, colourless and thus difficult to recognise. Adoral zone of membranelles usually 40–50% of body length, distally not overlapping on right margin. Buccal area flat and narrow. Buccal cirrus usually about at level of anterior portion of rather short paroral. Left frontal cirrus slightly displaced posteriad and somewhat larger than other two frontal cirri. One left and one right marginal row. Dorsal bristles short, that is, around 3 µm (except for *G. gonostomoidum* where they are 5 µm long, posteriorly up to 9 µm). At least some species common to very common in almost all types of terrestrial habitats; rarely in freshwater, usually under edaphic influence. Feed mainly on bacteria.

Remarks: See nomenclature before reading the remarks! For a foundation of the new, supposed phylogenetic position of *Gonostomum* and the gonostomatids, see remarks at the Gonostomatidae and *G. strenuum*. This new position and the acceptation of the gonostomatids is the main reason for anew treatment of *Gonostomum* within this monographic series. Further, since the publication of Berger (1999) several important papers on *Gonostomum* have been published (see list of synonyms and chapter below), the number of species assigned has increased from four to eight (plus one incertae sedis), and some chapters in the first review are not as detailed as necessary. Here I provide a new, updated, much more complete list of synonyms

containing, inter alia, the original descriptions, the review by Berger (1999), papers overlooked by Berger (1999), and works published after 1999.

The history of *Gonostomum* is complex due to some serious nomenclatural and taxonomic mistakes made by previous authors. Sterki (1878) established *Gonostomum* for the *Oxytricha affinis* described by Stein (1859). Interestingly, Stein himself discussed an intermediate position of *O. affinis* between *Oxytricha* Bory de Saint-Vincent in Lamouroux et al., 1824 and *Stichotricha* Perty, 1849 (Stein 1859, p. 187), a relationship not supported by later authors. Kent (1882) established *Plagiotricha* for *Oxytricha strenua* described by Engelmann (1862) because it differs from all other *Oxytricha* species by the oblique arrangement of the ventral cirral rows. He also discussed that Sterki (1878) already has established *Gonostomum* for *O. affinis*, but did not accept this genus-group name, inter alia, because of the resemblance with the names of some metazoan taxa (*Gonostoma*, *Gonostomus*). Thus, he transferred *O. affinis* to *Plagiotricha*, but simultaneously overlooked that the name proposed by himself (*Plagiotricha*) is a homonym of *Plagiotricha* Bory de Saint-Vincent in Lamouroux et al., 1824 (see Berger 2001, p. 72).

Maupas (1883, p. 550) transferred the marine species *Stichochaeta pediculiformis* Cohn, 1866[1] to *Gonostomum*, a classification not confirmed by later studies (see below). In contrast to Maupas (1883), Gourret & Roeser (1888) classified *Stichochaeta pediculiformis*, *Oxytricha affinis*, and *O. strenua* – but not the type species *Stichochaeta cornuta* Claparède & Lachmann, 1858 – in *Stichochaeta*, that is, they put *Gonostomum* and *Plagiotricha* Kent, 1882 into the synonymy of *Stichochaeta*. However, they overlooked that such a procedure is nomenclaturally impossible, that is, one cannot accept a genus without inclusion of the type species.

Bütschli (1889) accepted *Gonostomum* and put *Plagiotricha* Kent, 1881 into its synonymy. Further, he supported Maupas' (1883) decision to include *Stichochaeta pediculiformis* in the present genus. Consequently, Bütschli (1889), who classified *Gonostomum* in the Pleurotrichinae (a subfamily of the oxytrichids), accepted three species, namely, *G. affine*, *G. strenua*, and *G. pediculiformis*.

Kahl (1932) accepted the synonymy of *Gonostomum* and *Plagiotricha*, but made no comment about the type species and included only two species, namely *G. strenuum* and *G. affine*. However, Kahl (1932, p. 596) recognised that *S. pediculiformis* neither belongs to *Stichochaeta* (= *Stichotricha*) nor to *Gonostomum* and therefore transferred it to the new genus *Trachelostyla*. Unfortunately, he forgot to fix a type species so that his genus became never valid (for details see Berger 2008, p. 474).

Kudo (1950) and Corliss (1961) classified *Gonostomum* in the oxytrichids, obviously referring to Kahl (1932). However, Kahl's classification is undifferentiated be-

[1] *Stichochaeta* Claparède & Lachmann, 1858, with the limnetic *Stichochaeta cornuta* Claparède & Lachmann, 1858 as type species, is a junior synonym of *Stichotricha* Perty, 1849 as already recognised by Stein (1859, p. 176) and later confirmed and accepted by several prestigious taxonomists (e.g., Bütschli 1889, p. 1743; Kahl 1932, p. 559, 596; Borror 1972, p. 12; Foissner et al. 1991, p. 210).

cause he assigned all genera to the Oxytrichidae, except those belonging to the euplotids and aspidiscids.

As mentioned in the nomenclature section, Borror (1972, p. 14) incorrectly assumed that *Oxytricha strenua* is the type of *Gonostomum* due to monotypy. Simultaneously he transferred the true type – *Oxytricha affinis* – to *Gastrostyla* Engelmann, 1862 and therefore unconsciously synonymised *Gonostomum* with *Gastrostyla*[1]. Interestingly, Borror (1972, p. 15) assigned the *Gonostomum* species described by Gellért (1956a, 1957), which closely resemble *G. affine*, to *Trachelostyla*, that is, he allocated the *Gonostomum* species to three genera (*Gonostomum*, *Gastrostyla*, *Trachelostyla*) which he classified in the Oxytrichidae.

Buitkamp (1977) basically took over the oxytrichid classification proposed by Borror (1972), but removed *O. affinis* from *Gastrostyla* and transferred it to *Trachelostyla*, a genus already proposed by Kahl (1932), but validated just 40 years later by Borror (1972) due to the fixation of *Stichochaeta pediculiformis* as type species (for review, see Berger 2008, p. 474). Like Borror (1972), Buitkamp (1977) obviously incorrectly confined *Gonostomum* to *G. strenuum*.

Unfortunately, Borror's (1972) incorrect statement about the typification in *Gonostomum* was taken over by Jankowski who put *Gonostomum* in the Oxytrichinae, one of three subfamilies (Ancystropodiinae, Psammomitrinae) of the Oxytrichidae (Jankowski 1979, p. 77). By contrast, Stiller (1974), Corliss (1977, 1979), and Tuffrau (1979, 1987) put *Gonostomum* into the Holostichidae, an assignment difficult to comprehend from the morphological point of view, because this group has – like the other urostyloids – distinct midventral cirri (for review, see Berger 2006a, p. 84). However, some molecular analyses indicate that *Holosticha* – as defined by Berger (2003, 2006a) – does not belong to the other urostyloids (e.g., *Urostyla*, *Pseudokeronopsis*, *Anteholosticha*), but branch off at the base of the Hypotricha tree (e.g., Paiva et al. 2009). Later, Tuffrau also classified *Gonostomum* in the oxytrichids (Tuffrau & Fleury 1994). Corliss (1979) was also uncertain about the classification in the holostichids and supposed that it could belong to the oxytrichids. As already mentioned in the nomenclature section, Jankowski (1979, p. 62) incorrectly assumed that *O. affinis* is the type species of *Plagiotricha* Kent, 1882.

Hemberger (1982) reviewed *Gonostomum* and mentioned, without discussion, *G. affine* as type species, likely because he put *G. strenuum* – after long hesitation – into the synonymy of *G. affine*. Hemberger (1982, p. 261) also discussed the morphological resemblance with *Trachelostyla*, but finally accepted both genera because the adoral zone of the proter is newly formed in *T. pediculiformis* (vs. taken over from parental specimen in *G. affine*) as briefly reported by Kool (1970) and later confirmed by Shao et al. (2007; for review, see Berger 2008, p. 474). Hemberger (1982) accepted the comprehensive synonymy of *G. affine* proposed by Buitkamp

[1] It is nomenclaturally impossible to transfer the type species (e.g., *Oxytricha affinis*) of a genus (e.g., *Gonostomum*) to another genus (e.g., *Gastrostyla*) by simultaneous acceptance of the detypified genus (*Gonostomum*). For review of *Gastrostyla*, see Berger (1999, p. 789) and Berger (2008, p. 138).

(1977) and therefore *Gonostomum* is monotypic in his revision. He classified both *Gonostomum* and *Trachelostyla* in the oxytrichids.

Foissner (1982) made a brief comment about *Gonostomum* and *Trachelostyla*. He accepted, with reference to Hemberger (1982), both genera and described *G. franzi*, a species with about 12 macronuclear nodules (see *Neowallackia franzi*, p. 281).

Curds et al. (1983, p. 406, 416) significantly increased the confusion as concerns the genera *Gonostomum* and *Trachelostyla*. Unfortunately, they completely wrest the meaning of the two names. For *Gonostomum* they provided an illustration of *Trachelostyla pediculiformis*, type of *Trachelostyla* (Fig. 97k in Berger 2008) whereas they illustrated *Gonostomum ciliophorum*, a synonym of the type species *G. affine*, as representative for *Trachelostyla* (Fig. 118h in Berger 1999).

Fortunately, Maeda & Carey (1984) somewhat moderated the muddle in that they provided a comprehensive review of the genera *Trachelostyla* and *Gonostomum*. They discussed in detail, inter alia, the history of these two taxa. Regrettably, they made no comments on the type species, the major reason for the permanent nomenclatural and taxonomic problems in these genera. In addition, they assigned neither *Trachelostyla* nor *Gonostomum* to a higher taxon. Perhaps they agreed with the classification in the Holostichidae proposed, inter alia, by Corliss (1979).

Small & Lynn (1985) established the family Gonostomatidae comprising *Gonostomum*, *Wallackia*, and *Trachelochaeta* (Table 3; further details see p. 51ff). Unfortunately, they also detypified *Gonostomum* because they classified *O. affinis* in *Trachelostyla*. As an example for *Gonostomum* they mentioned *G. franzi*, a species classified in *Neowallackia* in the present book.

Berger & Foissner (1997) and Berger (1999) classified *Gonostomum* in the oxytrichines because of the similarity with 18-cirri hypotrichs. At that time I supposed that the 18-cirri pattern is an apomorphy of the oxytrichids. In addition, we deduced the simple dorsal kinety pattern of *Gonostomum* (three bipolar kineties) from the complex *Oxytricha*-pattern (bipolar kineties plus fragmentation plus dorsomarginal kineties) via a loss of the fragmentation and the dorsomarginal kineties. However, a new interpretation of the morphological and ontogenetic features and a contradiction with molecular data required a new hypothesis. For details, see Gonostomatidae (p. 51) and Berger (2006a, 2007, 2008, 2008a).

Shi (1999) and Shi et al. (1999) assigned *Gonostomum* to the Keronopsidae Jankowski, 1979, together with *Keronopsis*, *Parakeronopsis*, *Erniella*, *Cladotricha*, *Pseudouroleptus*, *Pelagotrichidium*, *Wallackia*, and *Paraurostyla*. Since the paper is in Chinese I do not know the foundation for this classification. However, at least the inclusion of *Paraurostyla* – with its fragmenting dorsal kinety and the dorsomarginal rows – very clearly shows that the keronopsids sensu Shi are not monophyletic. *Keronopsis* and *Paraholosticha* species are the sole hypotrichs which divide in cysts (e.g., Garnjobst 1937, Dieckmann 1989), a further hint that the classification proposed by the Chinese workers is not ultimate. In addition, they incorrectly mention *G. strenuum* as type species of *Gonostomum* (see above).

In contrast to Small & Lynn (1985), Lynn & Small (2002) classified *Gonostomum* in the Trachelostylidae (together with *Trachelostyla*, *Terricirra*, *Hemisincirra*, and *Lamtostyla*), that is, they synonymised the gonostomatids with the trachelostylids (Table 14 in Berger 2008). Unfortunately, they made the same nomenclatural mistake as in 1985 in that they assigned *G. affine*, type of *Gonostomum*, to *Trachelostyla*, an approach which is nomenclaturally not possible (see above). As example for a member of *Gonostomum* they mention, like Shi et al. (1999), *Gonostomum strenuum*.

Jankowski (2007) has corrected his previous mistakes (Jankowski 1979) concerning the type species for *Gonostomum* and *Plagiotricha*. Interestingly, he activated *Plagiotricha* Kent, 1882 and classified both genera in the oxytrichids. I did not translate the Russian text and therefore I do not know the foundation for the validation of Kent's genus. Obviously *Plagiotricha* is monotypic in Jankowski's revision. I suggest that molecular data on *G. affine* should be awaited to get a better insight into the relationships of *G. affine* and *G. strenuum*. When they reliable disprove the close affinity indicated morphologically, then *Plagiotricha* could be indeed reactivated. Unfortunately, *Plagiotricha* Kent, 1882 is a junior homonym of *Plagiotricha* Bory de Saint-Vincent in Lamouroux et al., 1824. Whether or not the older *Plagiotricha* is indeed valid needs a detailed analysis because no type species was fixed in the original description (Aescht 2001, p. 127).

The latest classification of *Gonostomum* was provided by Lynn (2008). He followed the second edition of the ciliate guide and included it in the Trachelostylidae, that is, he maintained the synonymy of the gonostomatids and trachelostylids proposed by Lynn & Small (2002).

For a comparison with other genera classified in the gonostomatids, see remarks at the Gonostomatidae, key, and remarks section at the other genera. The species section below contains all species presently assigned to *Gonostomum*. However, for the species already reviewed in the first volume of the monographic series, only some remarks and new data are provided and the reader is therefore mainly referred to Berger (1999) as concerns morphological description, illustrations, and details about occurrence and ecology. Consult this book also for *G. parvum* Lepsi, 1947 – classified as species indeterminata – and insufficient redescriptions of various *Gonostomum* species (Berger 1999, p. 393, 395).

Acosta-Mercado & Lynn (2003, p. 370; 2004, p. 585) found indeterminable *Gonostomum* species in soil samples from close to *Bromelia pinguin* in the Camabalache Commonwealth Subtropical Moist Forest in Western Puerto Rico.

Morphogenesis in *Gonostomum* (Table 15): *Gonostomum* is a group of 18-cirri hypotrichs with three noteworthy features concerning the cirral pattern: (i) the postoral ventral cirri are right of the adoral zone (not behind the oral apparatus/adoral zone as insinuated by the term itself); (ii) the number of 18 frontal-ventral-transverse cirri is more or less distinctly reduced (most species) or somewhat increased (*G. strenuum*, *G. gonostomoidum*, *G. terrestre*); and (iii) the number of frontal-ventral-transverse cirri is rather variable. These features and the small size of most

species make it rather difficult to study the cell division in detail, that is, to find the exact origin of the individual anlagen, the most interesting part of an ontogenetic sequence. The origin of the anlagen I–VI of the oxytrichids was compiled by Berger & Foissner (1997) and Berger (1999, p. 64). *Gonostomum* – which was classified in the oxytrichids in these papers – was not included, because primary primordia occur. The analysis revealed a lot of highly interesting features, for example, that in the proter an anlage usually originates from a parental structure which itself originated from the same anlage (e.g., anlage II originates from cirrus II/2 [= buccal cirrus]; anlage III originates from parabuccal cirri [= cirrus III/2). However, there exist some important exceptions from this rule, for example, anlage VI never originates from the parental frontoterminal cirri (cirri VI/3 and VI/4), but are formed from anlage V or de novo (Table 4 in Berger 1999). In the opisthe, the situation is rather similar, except for anlagen I–III which almost invariably originate from the oral primordium, because no parental structures of I–III are present in the morphogenetic active area of the opisthe.

Four species – *G. affine*, *G. algicola*, *G. kuehnelti*, and *G. strenuum* – have been investigated ontogenetically so far (Table 15). Unfortunately, most studies do not allow to reconstruct the exact origin of the anlagen I–VI, because it is very difficult to follow the process in detail in these relatively small species. In addition, the parental frontal-ventral cirri, from which most anlagen originate, are concentrated in the area right of the adoral zone so that the distances between the individual structures are very small. Thus, it is recommended to concentrate on this topic when species are restudied.

Gonostomum species produce so-called primary primordia in early stages of cell division. These are common anlagen for proter and opisthe, which later divide to form the individual ("secondary") anlagen for both filial products. This type of primordia is also known from *Urosoma* (Foissner 1983a) and *Tachysoma* (Hemberger 1982), and therefore we hypothesised that these three genera are closely related (Berger & Foissner 1997, Berger 1999). Now I am no longer convinced that this assumption is correct, because these genera differ significantly, inter alia, in their dorsal morphogenesis (for review, see Berger 1999).

Species included in *Gonostomum* (alphabetically arranged basionyms are given): (1) *Gonostomum albicarpathicum* Vd'ačný & Tirjaková, 2006a; (2) *Gonostomum algicola* Gellért, 1942; (3) *Gonostomum kuehnelti* Foissner, 1987c; (4) *Gonostomum namibiense* Foissner, Agatha & Berger, 2002a; (5) *Oxytricha affinis* Stein, 1859 (type species); (6) *Oxytricha strenua* Engelmann, 1862; (7) *Trachelochaeta gonostomoida* Hemberger, 1985; (8) *Trachelochaeta terrestris* Alekperov, 2005. Incertae sedis: (9) *Urosoma macrostoma* Gellért, 1957.

Species misplaced in *Gonostomum*: The species listed below have been transferred to *Gonostomum*. However, new data and/or distinct differences to the cirral pattern of the type species *G. affine* show that they are very likely misplaced in the present genus.

Gonostomum ambiguum in Enriques (1913, p. 105, 109). Remarks: As already explained in the "Catalogue of ciliate names" (Berger 2001, p. 29), I do not know the "original description" of *G. ambiguum*. Probably it is a provisional name or an unintended combination of *Trichoda ambigua* Müller, 1786 – popularly known as *Spirostomum ambiguum* (Müller, 1786) Ehrenberg, 1833 – with *Gonostomum*. Found in the surroundings of the city of Bologna, Italy.

Gonostomum corsica (Gourret & Roeser, 1888) Hamburger & Buddenbrock, 1929 (basionym: *Stichochaeta corsica* Gourret & Roeser, 1888, Archs Biol., 8: 187). Remarks: This species is, according to Hamburger & Buddenbrock (1929, p. 93), very likely a junior synonym of *Trachelostyla pediculiformis* (for review, see Berger 2008, p. 478). Simultaneously, Hamburger & Buddenbrock (1929, p. 94) transferred it to *Gonostomum*, a classification not favoured at present.

Gonostomum franzi Foissner, 1982. Remarks: Now type species of *Neowallackia* (see p. 281).

Gonostomum mereschkowskii (Andrussowa, 1886) ?Lepsi, 1926 (basionym: *Stichochaeta mereschkowskii* Andrussowa, 1886, Trudy imp. S-petersb. Obshch. Est-est., 17: 244). Remarks: In 1999 I wrote that I do not know the original description of "*Gonostomum mereschkowskii*" briefly mentioned by Lepsi (1929, p. 297), and I supposed that it is very likely a nomen nudum, that is, a new species without description (Berger 1999, p. 368). However, soon afterwards I recognised that this is a combination of *Stichochaeta mereschkowskii* with *Gonostomum* (Berger 2001, p. 80), but I overlooked that this combination was already used by Lepsi in an earlier paper (Lepsi 1926, p. 86). Unfortunately, it is rather difficult to find out the true author of this combination. Perhaps it is Bütschli (1889, p. 1748), who mentioned the paper by Andrussowa (1886), although with doubt, in the genus section of *Gonostomum*, indicating that he considered *Stichochaeta mereschkowskii* as a member of this genus. On the other hand, Bütschli wrote that *Gonostomum* comprises three species, namely, *G. affine*, *G. strenuum*, and *G. pediculiformis* (now *Trachelostyla pediculiformis*; for review, see Berger 2008, p. 478) meaning that he did not transfer *S. mereschkowskii* to *Gonostomum*. The next authors which come into question are Lepsi (1926, p. 86) and Hamburger & Buddenbrock (1929, p. 94); perhaps they figured that Bütschli (1889) already has made this combination. *Stichochaeta mereschkowskii* is not only misplaced in *Gonostomum*, but also in *Stichochaeta*, a junior synonym of *Stichotricha* Perty, 1849 (e.g., Stein 1859, Kahl 1932). Kahl (1932, p. 581, figure legend) therefore introduced the genus-group name *Gastrosticha* for this curious and little known species which will be treated in the volume where the spiralled taxa are reviewed because the illustration by Andrussowa (1886) indicates that the cirral rows are very heavily twisted.

Gonostomum pediculiforme (Cohn, 1866) Maupas, 1883 (basionym: *Stichochaeta pediculiformis* Cohn, 1866, Z. wiss. Zool., 16: 285, 299). Remarks: This is the type species of *Trachelostyla* Borror, 1972, a marine genus revised by Berger (2008, p. 474).

Oxytricha (Opisthotricha) elongata Grandori & Grandori, 1934. Remarks: Berger (2008, p. 477) supposed that this little known species will be briefly treated in a supplement to *Gonostomum*. However, the habitus and especially the long caudal cirri are more reminiscent of *Trachelochaeta bryophila*, than on *Gonostomum* species (Fig. 56a–c). Thus, I preliminary put it into *Trachelochaeta*, however, without formal combination (see p. 306).

Key to *Gonostomum* species

Identification of *Gonostomum* species is difficult and should be confirmed by protargol preparations, especially in the group with postorally extending frontoventral cirri. Note that *G. terrestre* and *Urosoma macrostomum* are only insufficiently described so that the key is probably inexact for these taxa. If you find a *Gonostomum*-like population with tailed body and lacking transverse cirri, see *Paragonostomum*. When the postoral area bears two cirral rows (except the marginal rows), see *Wallackia* and *Neowallackia*. All these species have a gonostomatid oral apparatus (Fig. 3a).

1 Posterior body end more or less distinctly tailed (Fig. 22a–j). . . . . *Gonostomum namibiense* (p. 140)
- Posterior body end not distinctly tailed. **2**
2 Two macronuclear nodules. **4**
- More than 2 macronuclear nodules. **3**
3 Four (3–6) macronuclear nodules (Fig. 21a–j) . . . . . *Gonostomum albicarpathicum* (p. 135)
- 10–19, usually about 14 macronuclear nodules (Fig. 123a–f in Berger 1999; Fig. 15a–c). . . . . *Gonostomum kuehnelti* (p. 109)
4 (2) Postoral area without frontoventral cirri (e.g., Fig. 18a, b, 3a). **5**
- Frontoventral cirri extending onto postoral area[1] (Fig. 23a, d, i, 25a, 26a). **8**
5 Paroral composed of 3–6, usually 4 cilia (Fig. 18a, b, q). . . . . *Gonostomum algicola* (p. 116)
- Paroral composed of 5 or more, usually more than 10 cilia (e.g., Fig. 3a). **6**
6 Paroral composed of 5–20, usually about 9–14 cilia; usually 11 (sometimes a little less) frontal-ventral cirri on frontal area (e.g., Fig. 3a, 11j, 12a–f). . . . . *Gonostomum affine* (p. 68)
- Paroral likely composed of more than 20 cilia (values uncertain), that is, paroral rather long (Fig. 27a–c, 28a). **7**
7 Only 8 (variability not known) frontal-ventral[2] cirri on frontal area (Fig. 28a). . . . . *Urosoma macrostomum* (p. 168)

[1] Sometimes the cirri extend only very slightly behind the level of the buccal vertex (Fig. 23g).
[2] Frontal, buccal, frontoterminal, frontoventral, and "postoral" ventral cirri included.

- About 13 frontal-ventral cirri on frontal area (Fig. 27a–c). . . . . *Gonostomum* sp. 1 sensu Shin (1994; p. 166)

8 (4) Rightmost frontoventral row (= row of frontoterminal cirri)[1] terminates ahead of or about at level of buccal cirrus (Fig. 23d, i). *Gonostomum strenuum* (p. 146)

- Rightmost frontoventral row extends onto postoral area or even to the transverse cirri (Fig. 25a, 26a). **9**

9 Rightmost frontoventral row (row VI) extends to near transverse cirri (Fig. 26a). . . . . *Gonostomum gonostomoidum* (p. 158)

- Rightmost frontoventral row (row V?) terminates distinctly ahead of transverse cirri (Fig. 26a). . . . . *Gonostomum terrestre* (p. 164)

Gonostomum affine (Stein, 1859) Sterki, 1878

(Fig. 3a, 10a–m, 11a–m, 12a–f, 13a, 14a–n, 36k, Tables 2, 14, 15)

1859 ***Oxytricha affinis*. Stein**[2] – Stein, Organismus der Infusionsthiere, p. 186, Tafel XII, Fig. 1–6 (Fig. 10a–f; Fig. 117j–l in Berger 1999; original description; no type material available).

1878 ***Oxytricha affinis* St.** – Eyferth, Einfachste Lebensformen, p. 60 (guide to limnetic protozoa).

1878 ***Gonostomum affine*** – Sterki, Z. wiss. Zool., 31: 54, Tafel IV, Fig. 2 (Fig. 10g; combination with *Gonostomum*; schematic illustration of proximal portion of adoral zone).

1927 ***Gonostomum (Plagiotricha) affine* (Stein.)** – Sandon, Protozoan fauna of soil, p. 195, Plate VI, Fig. 15 (redrawing of Fig. 10d; monograph about soil protozoa).

1932 ***Gonostomum (Oxytricha) affine* (Stein, 1859)** – Kahl, Tierwelt Dtl., 25: 598, Fig. 113 $_{9}$, 115 $_{2-4}$, 116 $_{14, 23}$ (Fig. 10h in present book and Fig. 117v–z in Berger 1999; review, see remarks).

1936 ***Gonostomum affine* (Stein)** – Bhatia, Protozoa: Ciliophora, p. 372, Fig. 175 (redrawing of Sandon's 1927 redrawing of Fig. 10d; guide to protozoa of British India).

1956 ***Gonostomum spirotrichoides* n. sp.** – Gellért, Acta biol. hung., 6: 347, Abb. 12 (Fig. 118f in Berger 1999; original description of synonym; no formal diagnosis provided and likely no type material available).

1956 ***Gonostomum bryonicolum* n. sp.** – Gellért, Acta biol. hung., 6: 348, Abb. 6, 13 (Fig. 118g in Berger 1999; original description of synonym; no formal diagnosis provided and likely no type material available).

1956 ***Gonostomum ciliophorum* n. sp.** – Gellért, Acta biol. hung., 6: 348, Abb. 14 (Fig. 118h in Berger 1999; original description of synonym; no formal diagnosis provided and likely no type material available).

1957 ***Gonostomum geleii* n. sp.** – Gellért, Annls Inst. biol. Tihany, 24: 19, Fig. 4 (Fig. 118b in Berger 1999; original description of synonym; no formal diagnosis provided and likely no type material available).

1974 ***Trachelostyla canadensis* n. sp.** – Buitkamp & Wilbert, Acta Protozool., 13: 208, Abb. 6 (Fig. 117p in Berger 1999; original description of synonym; site where type slides deposited not mentioned, likely they are stored in the University of Bonn, Germany).

1982 ***Gonostomum affine* (Stein, 1859)** – Foissner, Arch. Protistenk., 126: 77, Abb. 18a–i, 62, 65, Tabelle 17 (Fig. 117a–i in Berger 1999; authoritative redescription. One protargol slide [accession

[1] Note that this row (= frontoterminal row = row VI) is separated from the postorally extending frontoventral row (= row V) by a more or less distinct gap (Fig. 23d, i).

[2] Stein (1859) provided the following diagnosis: Körper lineal-lanzettlich, nach vorn zugespitzt, mit vorragenden, am hinteren Körperende zusammenstossenden Randwimpern, sehr kurzborstigen, versteckten Afterwimpern und einem langen, schmalen, hinten knieförmig nach einwärts gekrümmten Peristom.

number 1981/86; Aescht 2003, p. 379; 2008, p. 140] is deposited in the Upper Austrian Museum in Linz [LI], see nomenclature and remarks).

1982 ***Gonostomum affine* (Stein, 1859) Sterki, 1878** – Hemberger, Dissertation, p. 190, Abb. 34a–j (Fig. 120a–j in Berger 1999; detailed revision of hypotrichs).

1994 ***Gonostomum affine* (Stein, 1859)** – Shin, Dissertation, p. 106, Fig. 15A–C, Table 13 (Fig. 119d–f in Berger 1999; description of Korean population).

1994 ***Gonostomum* sp. 2** – Shin, Dissertation, p. 119, Fig. 17A–C, Table 16 (Fig. 14l–n; description of Korean population; voucher slides[1] are deposited in the Department of Molecular Biology, Seoul National University, Korea).

1995 ***Gonostomum affine*** – Foissner, Ciliaten des Bodens, p. 184, Abb. 22, 23, 30–32 (Fig. 117a, h, 118q, 119b in Berger 1999; brief review).

1999 ***Gonostomum affine* (Stein, 1859) Sterki, 1878** – Berger, Monographiae biol., 78: 369, Fig. 20c, 21d, e, 117a–z, 118a, c–i, l–t, 119a–f, 120a–j, Tables 3, 23, 27 (detailed review).

1999 ***Gonostomum affine* (Stein, 1859) Sterki, 1878**[2] – Eigner, Europ. J. Protistol., 35: 37, Fig. 12–28, 33, Tables 1, 2 (Fig. 11a–m; cell division and comparison of three Styrian clones with a clone of *G. kuehnelti*).

2001 ***Gonostomum affine* (Stein, 1859) Sterki, 1878** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 51 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2001 ***Gonostomum affine* (Stein, 1859) Sterki, 1878** – Foissner, Stoeck, Schmidt & Berger, Acta Protozool., 40: 91, Fig. 1–5, 7–13, Table 1 (Fig. 12a–f, 13a; description of Austrian, Saudi Arabian, Namibian, Venezuelan, and Brazilian populations and comparison with *G. strenuum* using morphology and RAPD-fingerprinting).

2003 ***Gonostomum affine* (Stein, 1859) Sterki, 1878** – Dragesco, Trav. Mus. Hist. nat. Gr. Antipa, 45: 28, Fig. 47–49, Tableau 12 (Fig. 10i–m; description of Rwandan population).

2006 ***Gonostomum algicola* Gellért, 1942** – Kim & Shin, Korean J. syst. Zool., 22: 210, Fig. 1A–E, 2A–F, Tables 1, 2 (Fig. 14g–k; voucher slides of protargol-impregnated specimens are likely deposited in the private collection of M.K. Shin, University of Ulsan; description of Korean population; misidentification).

2008 ***affine Gonostomum* (Stein, 1859) Sterki, 1878** – Aescht, Denisia, 23: 140 (detailed catalogue about type material deposited in the Museum in Linz [LI]; see nomenclature).

2008 ***Gonostomum affine*** – Kamra, Kumar & Sapra, Indian J. Microbiol., 48: 380, Fig. 2a–c, 12a–h, Table 4 (Fig. 14a–c; description of Indian population).

2008 ***Gonostomum singhii* sp nov**[3] – Kamra, Kumar & Sapra, Indian J. Microbiol., 48: 376, Fig. 3a–d, 9a–e, Table 2 (Fig. 14d–f; original description of new synonym; one protargol slide is deposited in the Natural History Museum in London, UK; see nomenclature).

2009 ***Gonostomum affine*** – Foissner, Protozoological Monographs, 4: 218, Fig. 22, 23, 30–32 (Fig. 117a, h, 118q, 119b in Berger 1999; brief review).

Nomenclature: No derivation of the species-group name is given in the original description, the review by Berger (1999), or in any other paper. The name *affin·is, -is -e* (Latin adjective [m, f, n]; similar, related, bordering; Hentschel & Wagner 1996,

[1] Shin (1994) designated these slides as holotype and paratype; I suppose that these are incorrect terms for undescribed species.

[2] The improved diagnosis by Eigner (1999) is rather long and therefore not repeated here.

[3] Kamra et al. (2008) provided the following diagnosis: Average size of non dividers in vivo 71 × 26 µm, protargol stained cells 66 × 23 µm; cortical granules colourless and scattered; 1 contractile vacuole; 2 macronuclei, 2 micronuclei; adoral zone of membranelles 50% of body length, paroral membrane made of 14–16 widely spaced cilia, endoral membrane with tightly packed cilia; 17 fronto-ventral-transverse cirri – 1 buccal cirrus, 3 frontal cirri, 2 frontoventral cirri, 2 frontoterminal cirri, 3 postoral ventral cirri, 2 pretransverse ventral cirri, 4 transverse cirri; 1 left marginal row and 1 right marginal row; 3 dorsal kineties and 3 caudal cirri; cirri long and highly hypertrophied; ontogenesis in *Gonostomum* pattern.

p. 68) likely refers to the fact that the adoral zone runs along (borders) the cell margin. However, it cannot be excluded that Stein (1859) used this name because the species is, according to this author, closely "related" to *Stichotricha*. Type species of *Gonostomum* Sterki, 1878 by original designation (see genus section for details). Bonkowski (1996, p. 35) mistakenly assigned *G. affine* to "Buitkamp 1977". Unfortunately, Kamra et al. (2008) did not specify which slide (holotype or paratype) of the synonym *G. singhii* they deposited in the Museum in London.

The species-group name *spirotrichoides* is a composite of Spirotricha (a higher taxon of ciliates; a composite of the Greek nouns *he speira* [spiral] and *trichos* [hair] referring to the spiralled adoral zone of membranelles) and the suffix *-ides* (similar, especially in shape) because – according to Gellért (1956a) – the shape of the mouth, the course of the adoral zone, the lack of the lip, as well as the row of cilia fulfils the Spirotricha-character. The species group name *singhii* is derived from the term *singhi*, the local name of the common Indian food fish *Heteropneustus fossilis*, as the anterior membranelles of the adoral zone of the ciliate resemble the long barbles of the fish (Kamra et al. 2008).

From the following species-group names no derivation is given in the original descriptions. The name *bryonicolum* is a composite of the Greek noun *to bryon* (moss) and the Latin verb *colere* (to live in) and obviously alludes to the habitat (soil under moss) where the species was discovered. The name *ciliophorum* is a composite of the Latin noun *cilia* (cilia) and the Greek verb *phor-* (carry, bear); I do not know to which specific ciliary structure this non-specific ciliate name (all ciliates bear cilia!) shall refer. The name *geleii* is obviously a dedication to J. Gelei. The name *canadens·is, -is, -e* (m; f; n; living or occurring in Canada) indicates that this species was discovered in Canada. "*Trachelostyla candensis* Buitkamp and Wilbert, 1974" in Kim & Shim (2006, p. 210) is an incorrect subsequent spelling.

In 1999, I wrote that Foissner (1982) has deposited one slide of neotype specimens in the Upper Austria Museum in Linz (Berger 1999, p. 370). Unfortunately, I forgot to mention the source from where this information is. Foissner (1982) did not make any comment about the deposition of type or voucher material (see also Aescht 2008), and the first paper about the type material deposited in the museum in Linz was published by Aescht (2003). In addition, I found no other paper published between 1982 and 1999 where this information is contained. Perhaps I had an early version of Aescht (2003) or a personal communication from Foissner or Aescht. However, I also cannot exclude that I confused some information. Anyhow, Aescht (2003, p. 379) "confirmed" my comment that Foissner (1982) has deposited one neotype slide in the Upper Austrian Museum. Aescht (2008, p. 140) provided the neophoront (= neotype) with a question mark. Obviously, Foissner designated the slide 1981/86 as paratype which is incorrect because a paratype is – like the holotype – part of the type series (ICZN 1999, Recommendation 73D). However, the type series was studied, but not preserved by Stein (1859). In addition, the slide 1981/86 (or any other slide) was never the neotype slide because neither Foissner (1982), Berger (1999), nor anybody else published the qualifying conditions neces-

sary for neotypification (ICZN 1964, 1984, 1999; Article 75). In addition, the description and morphometry by Foissner (1982) is composed of several populations so that this material/description should not be used as neotype. *Gonostomum affine* is a very common, but rather variable species so that one cannot exclude that it is a sibling species complex (Berger 1999, p. 373; Foissner 2000, p. 72). Thus, neotypification of *G. affine* is highly recommended to define this species objectively. Preferably, the neotype should come from a population from the original type locality, that is, the Prokop-Tal, an area in the south-western suburbs of the city of Prague, Czech Republic (see occurrence and ecology).

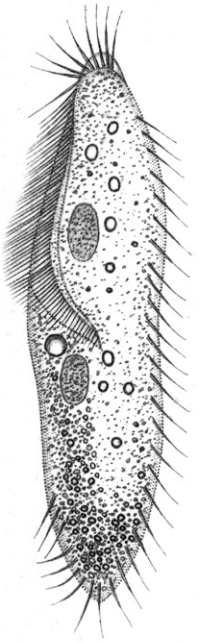
The misleading spelling *Gonostomum (Plagiotricha) affine* in Sandon (1927) does not mean that Sandon classified *Plagiotricha* as subgenus of *Gonostomum*, but should simple indicate that this species was assigned to *Plagiotricha* by a previous author (Kent 1882, p. 772). The same applies to *Gonostomum (Oxytricha) affine* in Kahl (1932), where *Oxytricha* refers to the generic assignment in the original description.

Remarks: The list above comprises only the original description, the combination with *Gonostomum*, the review by Kahl (1932), the original descriptions of the synonyms, most important redescriptions, the review by Berger (1999), papers overlooked by Berger (1999), and papers published 1999 or later. Thus, for a detailed list of pre-1999 synonyms and combinations, see Berger (1999, p. 369). For detailed comparison with *G. algicola* and *G. strenuum*, see p. 116, 146.

The taxonomy of this species is complicated mainly because the variability in body size and number of frontoventral, pretransverse ventral, and transverse cirri is rather high. Likely this plasticity and the commonness are the reason why eight synonyms have been described according to the monograph of oxytrichids (Berger 1999), where I simultaneously speculated that *G. affine* – as presently defined – is a complex of sibling species, an opinion also offered by Foissner (2000, p. 72). However, to unravel this problem comprehensive studies comprising, inter alia, a neotypification and morphometric, genetic, and relevant molecular analyses are needed. Studies on clonal cultures revealed that especially the number of transverse cirri (including pretransverse ventral cirri) differs distinctly between clones (on average 2.1 vs. 4.0 vs. 6.0; Eigner 1999).

In 1999, I did not discuss the nominal species individually and simply followed the synonymies proposed by Kahl (1932), Borror (1972), Buitkamp (1977), and accepted by Foissner (1982). The results by Foissner et al. (2002a), however, demonstrated that detailed morphological analyses can confirm the validity of some of the described species[1]. Perhaps, meaningful non-morphological methods will show that the relatively high morphological variability is due to the mixture of (morphologically) rather similar species. Thus, in the morphology section the synonyms are reviewed separately. A combination of morphological and RAPD-fingerprint analyses showed, however, that *G. affine*-morphotypes from Austria, Saudi-Arabia, Namibia,

[1] Foissner (1998, p. 203) also accepted the comprehensive synonymy proposed by previous workers, but simultaneously challenged the synonymies (Foissner 1998, p. 211, footnote 9).



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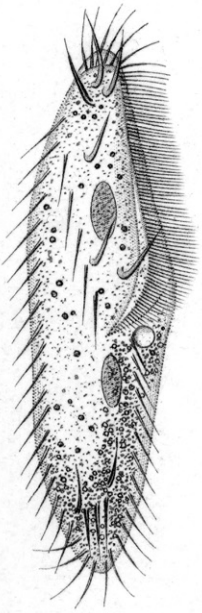

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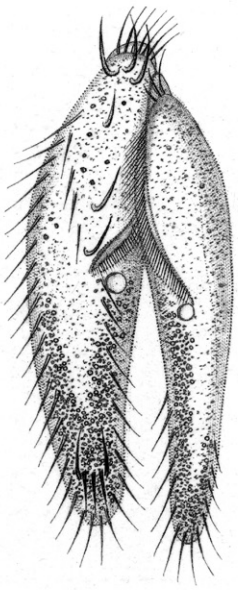

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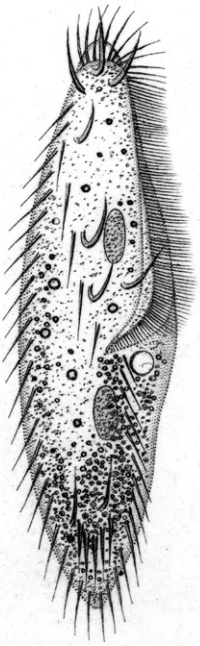

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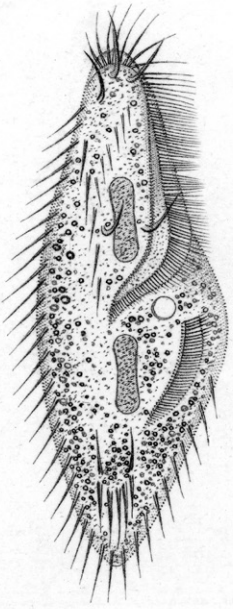

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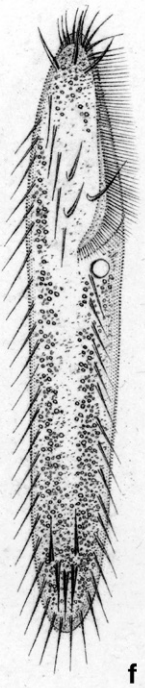

f

Venezuela, and Brazil fall into the range of the natural variability of a single species (Foissner et al. 2001).

Gonostomum spirotrichoides is one of three *G. affine* synonyms described by Gellért (1956a). He used live observation and Nigrosin preparations so that the data are likely reliable. The number of frontal-ventral-transverse cirri is not very strongly reduced. In total, only one postoral ventral cirrus and the leftmost transverse cirrus are lacking, referring to the 18-cirri pattern. Thus, the pattern is strongly reminiscent of that of *G. singhii*, a species recently described from a Himalayan valley. However, Kamra et al. (2008) counted only 14–16 paroral cilia (a value which agrees with that described for *G. affine*) in this Indian species whereas 22–25 cilia are obviously present in *G. spirotrichoides* (Fig. 118f in Berger 1999). This difference is almost as distinct as that between *G. affine* (usually around 13) and *G. algicola* (3–6, usually four). However, *G. spirotrichoides* is not described after protargol impregnation and therefore insufficiently characterised morphometrically; therefore, I preliminarily do not remove it from the synonymy of *G. affine*.

Gonostomum bryonicolum is the second synonym of *G. affine* described by Gellért (1956a; Fig. 118g in Berger 1999). He studied it in life and after sublimate fixation and opalblue preparation (Fig. 6 in his paper). The body shape, the cirral pattern, and the number of paroral cilia correspond very well with the data described for *G. affine*. By contrast, the four dorsal kineties, including the four caudal cirri, are rather unusual for *Gonostomum*, which (almost) invariably has the three bipolar kineties and caudal cirri taken over from the ground pattern of hypotrichs (Berger 2008). When detailed morphometric studies confirm the deviating dorsal pattern, then *G. bryonicolum* could be validated, either as species or at least as subspecies. Four dorsal kineties, but only three caudal cirri, are also reported for *Trachelostyla canadensis* (see below).

Gonostomum ciliophorum is the third species described by Gellért (1956a) which is presently classified as synonym of *G. affine* (Fig. 118h in Berger 1999). The body shape, the size, the cirral pattern, and the number of paroral cilia (around 10) are within the range of *G. affine*. The dorsal infraciliature is not known. Thus, *Gonostomum ciliophorum* cannot be separated reasonable from *G. affine*. The cirral pattern of *G. ciliophorum* is identical with that of *G. singhii*, recently discovered in soil samples from the Himalayan region (Kamra et al. 2008). This species was separated from the congeners mainly by the presence of two pretransverse ventral cirri and four transverse cirri. Kamra et al. (2008) compared *G. singhii* in detail only with *G. namibiense* (inter alia distinctly tailed) and *G. kuehnelti* (much more macronuclear nodules). From the type species, *G. singhii* was separated by the low variability of

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← **Fig. 10a–f** *Gonostomum affine* (from Stein 1859. From life). **a:** Dorsal view, largest specimens of type population 86–115 µm long. Parts of ventral infraciliature (adoral zone, marginal cirri), macronuclear nodules, contractile vacuole, and cytoplasmic inclusions are recognisable. **b:** Ventral view of specimen with three frontal cirri, one buccal cirrus, four frontoventral cirri, three postoral ventral cirri, two pretransverse ventral cirri, and three transverse cirri. **c, f:** Conjugating pair and post-conjugant. **d:** Ventral view of a specimen with 19 frontal-ventral-transverse cirri. **e:** Middle divider. Page 68.

the number and arrangement of frontal-ventral cirri. However, they obviously overlooked that populations with an identical pattern have been described previously by Gellért (1956a). Interestingly, both *G. ciliophorum* and *G. singhii* have rather strong and long cirri, according to the original descriptions. *Gonostomum spirotrichoides*, *G. bryonicolum*, and *G. ciliophorum* have the same type locality (see below), probably the main argument against their species status because it is unlikely that in the same, very localised area three different species of the *G. affine* group coexist.

Gonostomum geleii is the fifth *Gonostomum* species described by J. Gellért (Gellért 1942, 1956a, 1957). The specimen illustrated is spindle-shaped and has a rather strongly reduced number of frontal-ventral-transverse cirri, that is, 50% of the 18 cirri are lacking, inter alia, two or all "postoral ventral cirri", the pretransverse ventral cirri, and one transverse cirrus (Fig. 118b in Berger 1999). The paroral consists of 16 cilia which is within the range of *G. affine*. The dorsal ciliature (length of bristles; number of dorsal kineties and caudal cirri) is not known. Perhaps the illustration shows a starving specimen. At present there is no reason to remove *G. geleii* from the synonymy of *G. affine*.

Trachelostyla canadensis is the second youngest synonym of *G. affine*. Its cirral pattern agrees very well with that of the type species and likely for that reason the author himself synonymised these two species (Buitkamp 1977, p. 125). The major difference between *G. affine* and *T. canadensis* is in the number of dorsal kineties. Usually, *Gonostomum affine* has invariably three kineties (n = 126; Foissner et al. 2001), whereas Buitkamp & Wilbert (1974) originally described four kineties, however, without providing data about sample size and/or variability. Thus, this value should not be overinterpreted although it is interesting that Gellért (1956a) found the same number in *G. bryonicolum*. Further, *Trachelostyla canadensis* and *G. bryonicolum* have the same number of frontoventral cirri (each two [pseudo]rows[?] of three cirri; Fig. 117p, 118g in Berger 1999). However, they differ in the number of transverse and pretransverse ventral cirri (2 vs. 5) and caudal cirri (3 vs. 4); but note that in both cases no information about the variability is given. Foissner (1998, p. 210) synonymised *T. canadensis* with *G. algicola*, however, without providing a foundation. On p. 203 he synonymised *G. algicola* with *G. affine*, an act which he raised to question on p. 211 (footnote 9). The large adoral zone (about 50% of body length) and the two transverse cirri indicate that *T. canadensis* is not synonymous with *G. algicola*. Unfortunately, the most important feature for separation, namely the paroral, is obviously not illustrated in *T. canadensis* (Fig. 117p in Berger 1999).

Gonostomum singhii is classified as new synonym of *G. affine* in the present review (Fig. 14d–f). Kamra et al. (2008) stressed that it differs from the other *Gonostomum* species by the presence of invariably two pretransverse ventral cirri and four long and strong transverse cirri. They obviously used the monograph of the oxytrichids as reference book (Berger 1999) and therefore I am somewhat astonished that they did not discuss that *G. affine* itself (Fig. 119b in Berger 1999) as well as the *G. affine* synonyms *G. spirotrichoides* (Fig. 118f in Berger 1999) and *G. ciliophorum* (Fig. 118h in Berger 1999) have the same number of pretransverse ventral and trans-

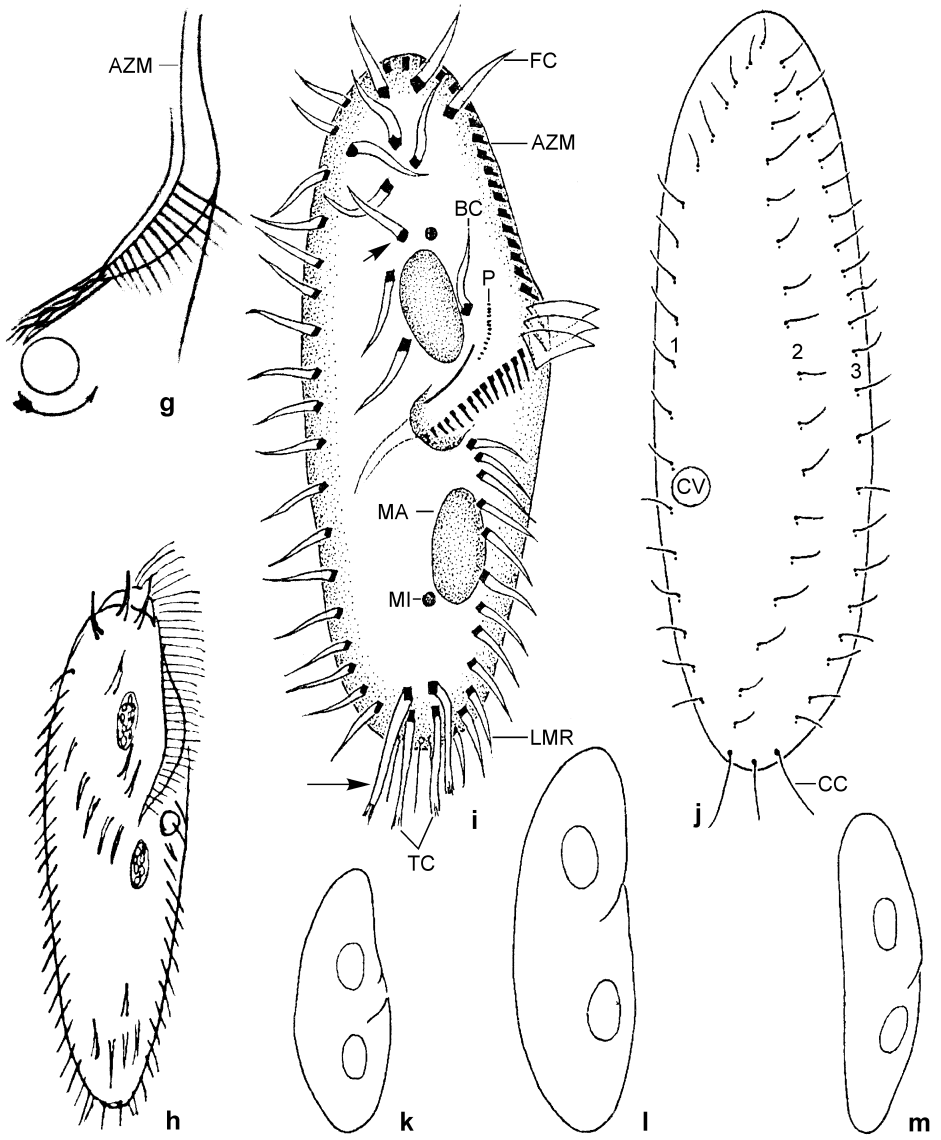

Fig. 10g–m *Gonostomum affine* (g, from Sterki 1878; h, after Stein 1859 from Kahl 1932; i–m, from Dragesco 2003. g, h, from life; i–m, protargol impregnation). **g:** Detail of proximal portion of adoral zone and cytopharynx; arrow marks rotation of food vacuole. **h:** Likely this is a relatively inexact redrawing of Stein's Fig. 10b. **i, j:** Infraciliature of ventral and dorsal side and nuclear apparatus of African population, 95 µm. Short arrow marks anteriormost postoral ventral cirrus (IV/2), long arrow denotes the right pretransverse ventral cirrus. **k–m:** Shape variants in ventral view, k = 92 µm, l = 134 µm (note that, according to Table 14, the largest specimen is 113 µm long), m = 110 µm. AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri, CV = contractile vacuole, FC = left frontal cirrus, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, TC = transverse cirri, 1–3 = dorsal kineties. Page 68.

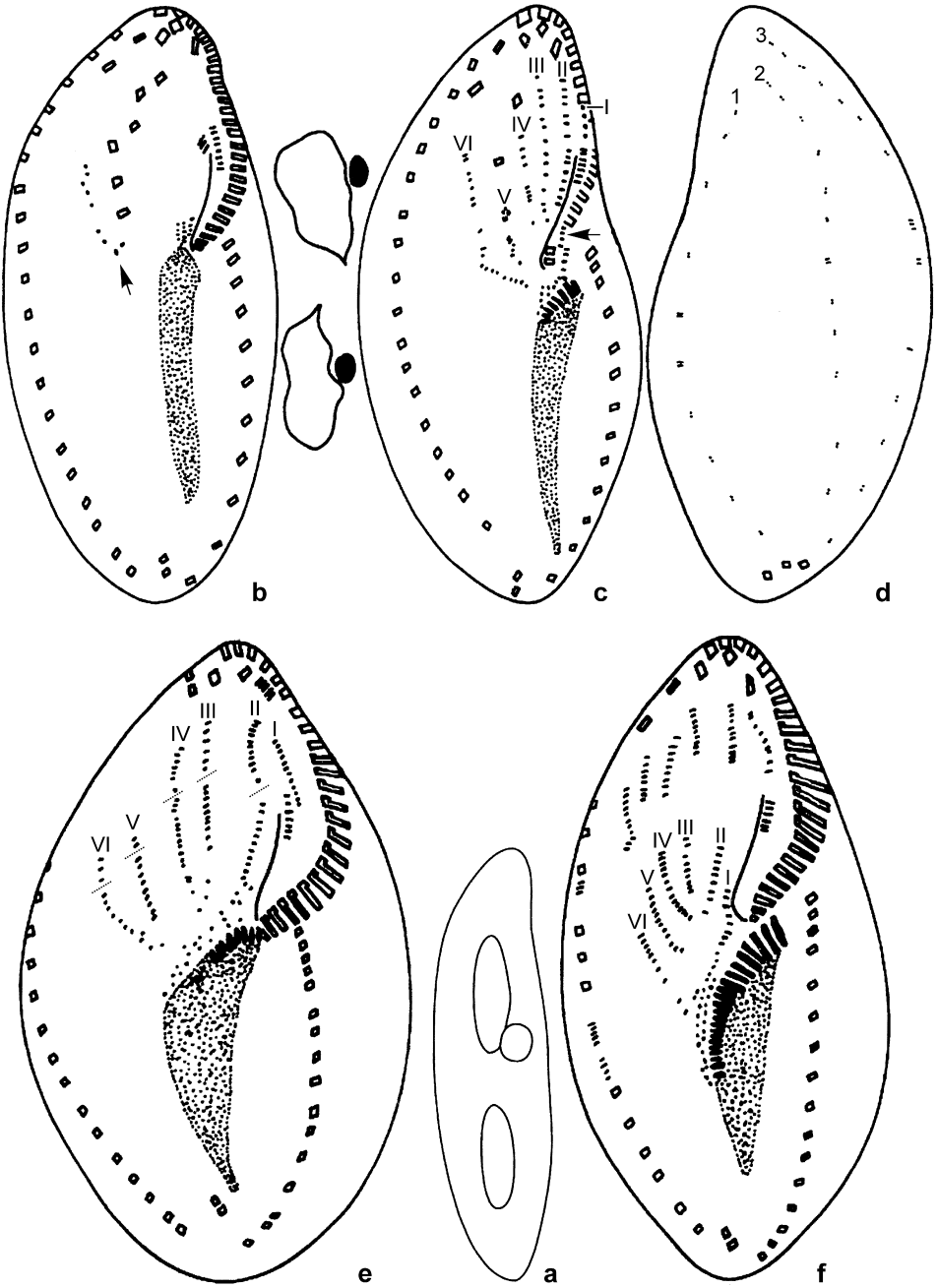

Fig. 11a–f *Gonostomum affine* (from Eigner 1999. a–f, clone II. a, from life; b–f, protargol impregnation). **a:** Body outline and nuclear apparatus of interphasic specimen in ventral view, 57 µm. **b:** Infraciliature of ventral side and nuclear apparatus of early divider, 62 µm. Arrow marks rear end of primary primordium VI which obviously originates de novo, that is, without contact to a parental cirrus or the oral primordium. Note that the buccal cirrus begins with the modification to primary primordium II. **c, d:** Infraciliature of

verse cirri. Simultaneously, they recognised the resemblance of *G. singhii* with clone IV of *G. affine* described by Eigner (1999, Fig. 11i–k), but they criticised that Eigner did not provide morphometric data. However, this is not quite correct because according to Table 2 in Eigner (1999) clone IV has 5–8 (n = 44), on average six (= 2 + 4) pretransverse ventral and transverse cirri, and the illustrated specimen in Eigner (1999) fits very well with the morphometric data provided by Kamra et al. (2008). Thus, *G. singhii* is very likely a synonym of *G. affine*. Kamra et al. (2008) compared the new Indian species also with *G. namibiense* (posterior body end distinctly tailed) and *G. kuehnelti* (10–17, on average about 14 macronuclear nodules), two species which can be rather easily distinguished from *G. affine*.

For the transfer of *G. andoi* Shibuya, 1929 and *G. affine* sensu Goodey (1911), two synonyms of the present species in Berger (1999), to *G. strenuum* see there. *Gonostomum affine* sensu Foissner (2000) is also assigned to *G. strenuum* (Fig. 23g, h). Kahl (1932) provided a redrawing (Fig. 10h) of one drawing of Stein's (1859) original description (Fig. 10b). However, the redrawing is rather inaccurate, especially as concerns the position of the frontal-ventral cirri. *Gonostomum affine* sensu Dragesco (2003) from Africa fits very well the other *G. affine* descriptions (Fig. 10i–m).

In 1999, I synonymised *Urosoma macrostomum* Gellért, 1957 with *G. affine* (Berger 1999, p. 370), however, without providing a foundation. Probably this proposal was premature and therefore this species is now preliminary affiliated to *Gonostomum* as incertae sedis until further data are available (p. 168). *Gonostomum algicola* sensu Kim & Shin (2006) is *G. affine* (see remarks of *G. algicola* for further details; Fig. 14g–k).

Gonostomum sp. 2 in Shin (1994; Fig. 14l–n) comes within the wide limits of *G. affine* and is therefore listed as synonym of the type species. The reduced number of frontal-ventral cirri indicates that one anlage (V?) is lacking in this population. However, further populations have to be studied to show whether or not this feature is stable. *Gonostomum parvum* Lepsi, 1947 was classified as species indeterminata by Berger (1999, p. 393), supposing that it is identical with *G. affine*. Finlay et al. (2001, p. 363) synonymised – although not formally – these two species.

Morphology: As discussed above, the systematics of *G. affine* is rather complicated. In the present chapter the original descriptions of the six synonyms are reviewed separately because future studies will perhaps show that one or two synonyms are valid species of the *G. affine*-complex. The chapter begins with a detailed

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← ventral and dorsal side of middle divider, 55 µm. Arrow marks anlage I for the opisthe, obviously an important difference to *G. kuehnelti* where anlage I of both filial products originates from a primary primordium, that is, a common anlage. **e:** Infraciliature of ventral side of middle divider, 48 µm. The primary primordia II–VI begin to separate into the anlage II–VI for the proter (ahead of oblique lines) and the opisthe (behind oblique lines). Note that anlage I originates independently from each other in proter and opisthe. **f:** Infraciliature of ventral side of middle to late divider, 50 µm. In both proter and opisthe six anlagen (I–VI; not labelled in proter) are recognisable. I–VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 68.

review of the original description by Stein (1859), who made very comprehensive live observations. For a summarising description of *G. affine* and some illustrations, see Berger (1999, p. 373).

Type population of *G. affine* Stein, 1859 (Fig. 10a–f): Body length of largest specimen 1/24 to 1/18 lines[1], that is, 86–115 µm; body length:width ratio 3.5–4.0:1. Body outline slender-lanceolate, margins converging anteriorly and strongly tapered, that is, with very narrowly rounded anterior end bearing a very small, blunt triangular frontal scutum; rear end more or less pointed; right body margin convex (Fig. 10d) or straight and somewhat curved inwards (Fig. 10a, b). Left cell margin with bluntly angular protrusion in mid-region; ahead of it the margin is straight, behind of it somewhat curved inwards. Dorsal side moderately vaulted, ventral side flat, with more or less sharp margins. Two macronuclear nodules, elongate ovoid and homogenous, anterior one almost in centre of frontal field, rear one close to buccal vertex. Micronucleus neither mentioned nor illustrated. Contractile vacuole close behind buccal vertex. Cortical granules neither mentioned nor illustrated. The description of the adoral zone corresponds exactly the gonostomatid pattern. According to Stein (1859), the oral apparatus of *G. affine* is strongly reminiscent of that of *Stichotricha secunda* (for detailed description of this species and its close relative *S. aculeata*, see Foissner et al. 1991, p. 203). Three frontal cirri, inconspicuously enlarged, triangularly arranged at anterior end of cell. One buccal cirrus near buccal lip. Two or three cirri (including cirrus III/2) in central portion of frontal field. Five or six cirri form oblique row extending from near anterior end of right marginal row to near buccal vertex; sometimes, Stein had the impression that this row continues posteriorly. No cirri behind adoral zone, except five transverse cirri, which are subterminally arranged and very fine and short and therefore not projecting beyond posterior body end; hence, they are difficult to recognise, inasmuch the posterior body region (and the left central body portion) is usually packed with greasily shining granules; according to Stein, the two outermost transverse cirri are often hook-shaped curved anteriorly, indicating that these two cirri are in fact pretransverse ventral cirri (Fig. 10b, c, f); further, Stein (1859) often had the impression that – besides the five

[1] In Ehrenberg (1838), Stein (1859), and some other early works the "Linie" (= line; abbreviated as: ‴) was used as measure of length of ciliates and other micro-organism. I checked the general parts of these books, but could not find a note about this topic. Unfortunately, this old measure is variable, that is, the size depends on the area where it was used (Hellwig 1988, p. 148). Further, it can be 1/12 inch (at duodecimal division) or 1/10 inch (at decimal division). Interestingly, the inch itself was variable at that time ranging from 2.3194 cm in Spain to 3.0 cm in Baden, Germany (Hellwig 1988, p. 264). The size for 1 line was as follows (Hellwig 1988): Saxonia 1.967 mm; England 2.116 mm; Prussia and Rhineland 2.18 mm; Vienna 2.2 mm; Paris 2.256 mm; Hesse 2.5 mm; Russia 2.54 mm; Wuerttemberg 2.865 mm. Ehrenberg and Stein worked mainly in the Prussia and Empire Austro-Hungary area (including Prague where Stein lived and worked; Lendl et al. 1977), indicating that 1 line in their papers is 2.18 mm or 2.2 mm. In Berger (1999, 2006, 2008) I used a conversion factor of 1‴ = 2.083 mm, a value not mentioned by Hellwig (1988). I do not know from where I have this factor, but since it is close to the 2.18 or 2.2 mentioned above I retain this value in the present and the following volumes of the monograph to ensure comparability of these old values. The resulting differences are negligible, inasmuch the life measurements are not very exact.

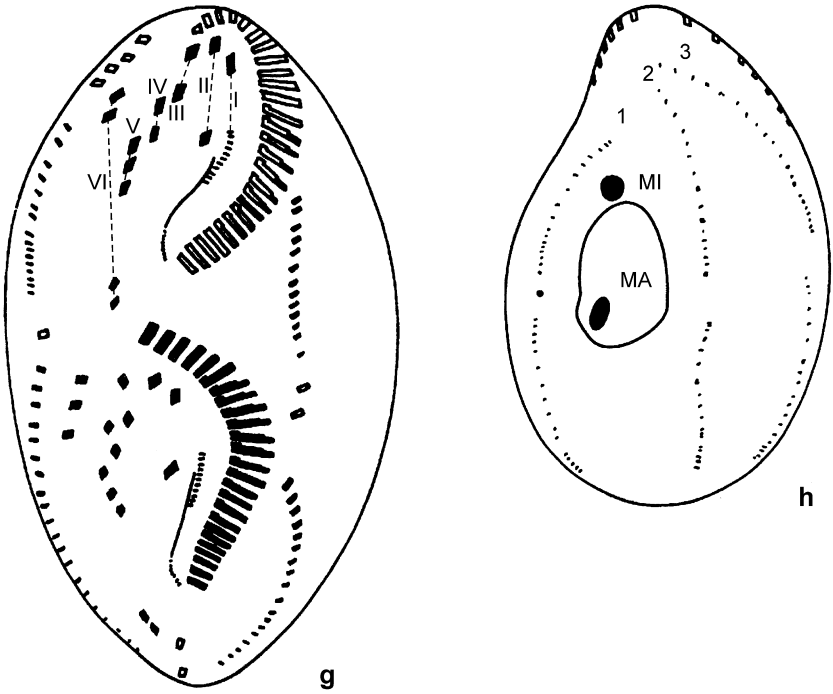


Fig. 11g, h *Gonostomum affine* (from Eigner 1999. Clone II after protargol impregnation). **g:** Infraciliature of ventral side of late divider, 55 µm. Cirri originating from same anlage are connected by broken line (only shown in proter). **h:** Infraciliature of dorsal side and nuclear apparatus of late divider, 46 µm. The lack of dorsomarginal kineties and kinety fragmentation shows that *Gonostomum* branched off rather early in the Hypotricha tree. MA = macronucleus, MI = micronucleus, I–VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 68.

transverse cirri[1] – an additional pair (= pretransverse ventral cirri) close to them is present (Fig. 10d, e); however, he was not quite sure about this feature. Marginal rows merge into each other posteriorly, indicating that Stein (1859) misinterpreted (justifiable) the caudal cirri as marginal cirri; cirri of right row protrude distinctly beyond cell margin, in left row only the rear half one does so; anterior half of left marginal row curved inwards and terminating at buccal vertex. Marginal cirri long, especially the rearmost one (caudal cirri?). Dorsal infraciliature not described.

Gonostomum spirotrichoides Gellért, 1956a (Fig. 118f in Berger 1999): Gellért studied the ciliates in life and after fixation and staining (Gellért 1956a, p. 341; 1956b, p. 81), but in the individual descriptions he did not provide details about the method used so that some data (e.g., body size, body shape) must not be overinterpreted. In the present case I suppose that he studied only one specimen, that is, no

[1] Fig. 117j in Berger (1999) is a redrawing of Fig. 4 on Plate XII of Stein (1859; Fig. 10d in present book). Unfortunately, I overlooked one transverse cirrus because at that time I did not have an original of Stein's monograph, but a xerox copy showing not all details.

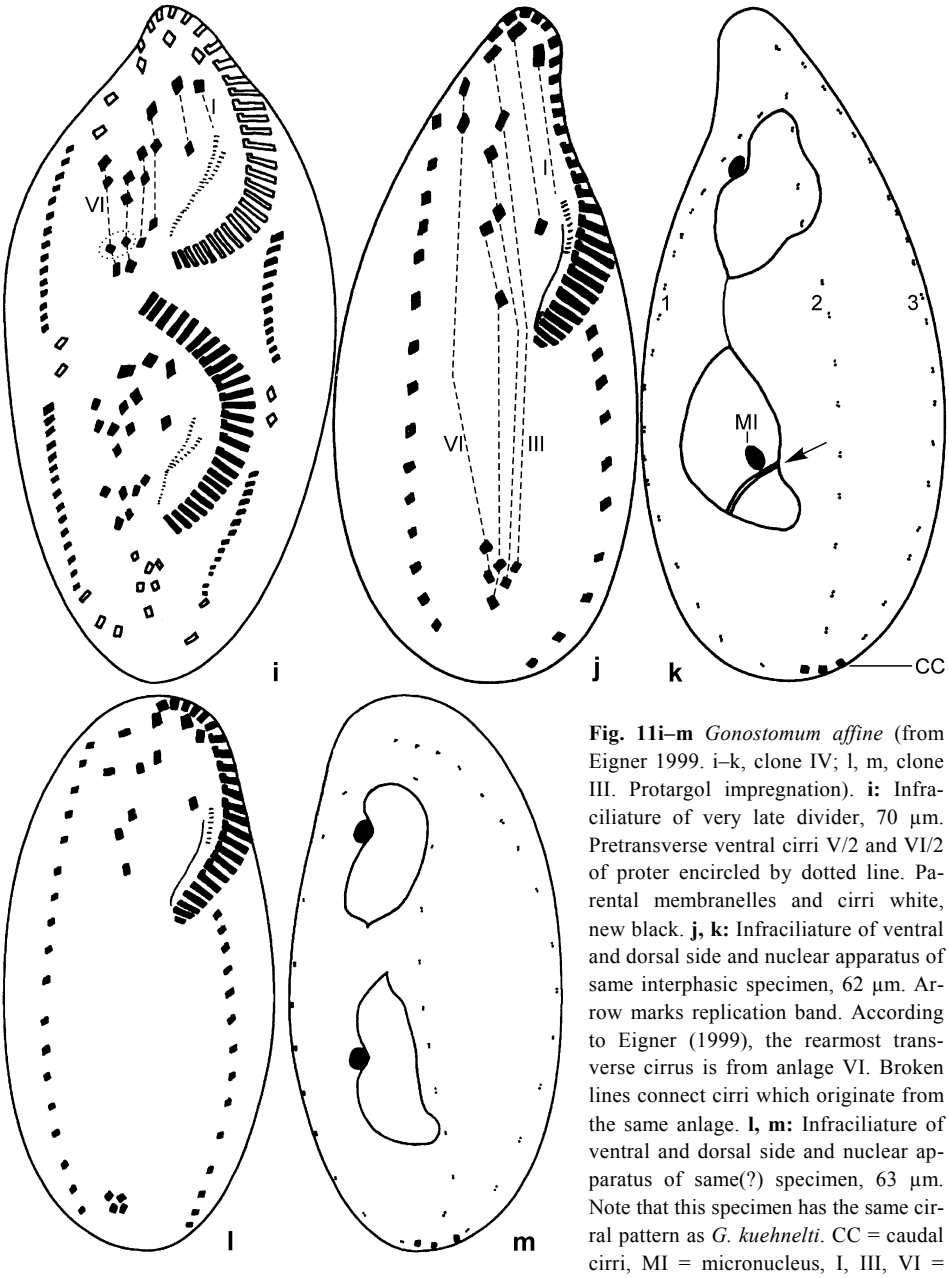


Fig. 11i–m *Gonostomum affine* (from Eigner 1999. i–k, clone IV; l, m, clone III. Protargol impregnation). **i:** Infraciliature of very late divider, 70 µm. Pretransverse ventral cirri V/2 and VI/2 of proter encircled by dotted line. Parental membranelles and cirri white, new black. **j, k:** Infraciliature of ventral and dorsal side and nuclear apparatus of same interphasic specimen, 62 µm. Arrow marks replication band. According to Eigner (1999), the rearmost transverse cirrus is from anlage VI. Broken lines connect cirri which originate from the same anlage. **l, m:** Infraciliature of ventral and dorsal side and nuclear apparatus of same(?) specimen, 63 µm. Note that this specimen has the same cirral pattern as *G. kuehnelti*. CC = caudal cirri, MI = micronucleus, I, III, VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 68.

data about the variability, especially of the cirral pattern, are known. Body length 110 µm; body length:width ratio of prepared specimen 4.1:1. Body cylindrical. Two

ovoid macronuclear nodules, each with one micronucleus; nodules slightly left of midline, each one in anterior and posterior half of cell. Contractile vacuole left of buccal vertex, contracts every 19–21 s. Cytoplasm bright, of green colour (reason not mentioned), contains many granules of substitute nutrients (stark? fat globules?). Presence/absence of cortical granules not mentioned. Adoral zone gonostomatid, occupies 50% of body length, composed of 27 membranelles; anteriormost four membranelles longer than remaining ones. Buccal field very narrow, more or less completely covered; "peristomial" lip (= buccal lip), however, lacking according to original description (but note that these details are difficult to recognise with ordinary bright field microscopy). One row of 22–25 relatively widely spaced cilia along right margin of proximal half of adoral zone; the fact that it is on the cell surface according to Gellért, indicates that this is the paroral; however, the row is rather long, that is, according to the illustration it extends from the buccal vertex to about 18% of body length which is ahead of the buccal cirrus; perhaps he mixed up paroral and endoral, and perhaps even lateral membranellar cilia. Pharyngeal fibres extend obliquely backwards. Three frontal cirri, left one – as is usual – somewhat displaced posteriorly. Buccal cirrus near anterior end of undulating membrane. Four frontoventral cirri in area behind right frontal cirrus and level of buccal cirrus. Two postoral ventral cirri right of proximal part of adoral zone. Two pretransverse ventral cirri and four transverse cirri. Right marginal row composed of 19 cirri in specimen illustrated, commences about at 11% of body length, only very slightly shortened posteriorly. Left marginal row composed of 15 cirri, commences at level of buccal vertex, terminates about at level of transverse cirri. Gap between marginal rows occupied by four caudal cirri, which are distinctly longer than the marginal cirri (about 14 µm long according to illustration). Three dorsal kineties with "long" bristles; unfortunately, length of bristles and arrangement of kineties neither mentioned nor illustrated; since only the ordinary number of three dorsal kineties is present, one of them must have produced two caudal cirri.

Gonostomum bryonicolum Gellért, 1956a (Fig. 118g in Berger 1999): See also first sentence at *G. spirotrichoides*. Body length 60 µm; length:width ratio of prepared specimen 2.7:1. Body oval, cylindrical[1]. Two macronuclear nodules slightly left of midline, each one in anterior and posterior half of cell; each nodule with one micronucleus. Contractile vacuole could not be observed. Presence/absence of cortical granules neither mentioned nor illustrated. Cytoplasm bright, greenish (reason not mentioned). Adoral zone gonostomatid, occupies 58% of body length in specimen illustrated, composed of 26 membranelles[2]; membranelles extending along left cell margin mainly (75%) laterally and not ventrally. Buccal field moderately large, pharynx extends almost transversely rightwards. Paroral composed of 16 widely spaced cilia along margin of buccal lip. Endoral not described. Three "strong" fron-

[1] Gonostomatids and other typical hypotrichs are not truly cylindrical, but more or less distinctly flattened dorsoventrally. Perhaps Gellért observed an inflated specimen.

[2] According to Gellért (1956b), the membranelles are "double". Perhaps the cilia of the two long basal body rows (rows 1 and 2 in Fig. 8 of Berger 1999) have split off? The rather large relative length of the adoral zone (58%) indicates that this is a premature postdivider.

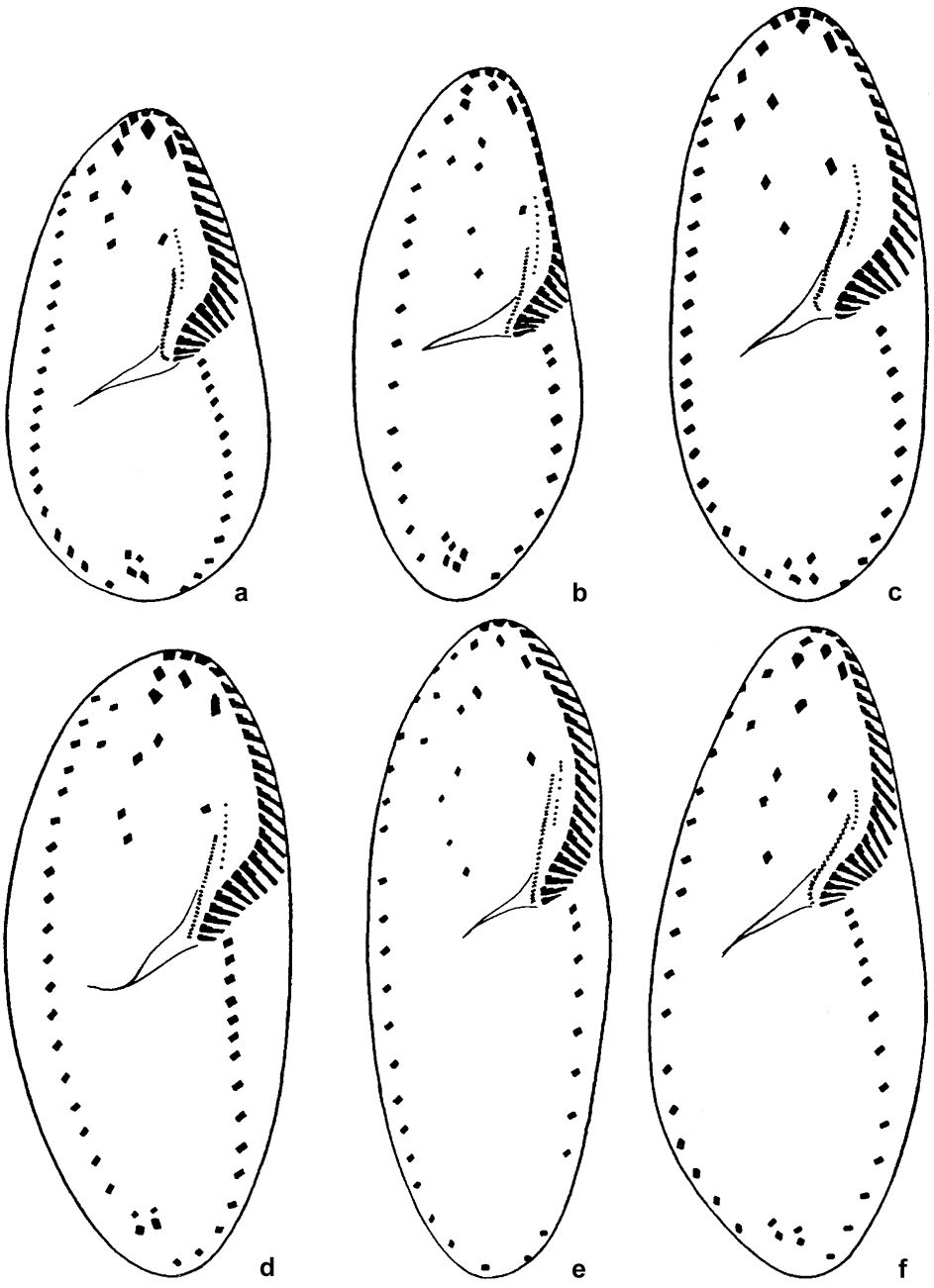


Fig. 12a–f *Gonostomum affine* (from Foissner et al. 2001. Protargol impregnation). Infraciliature of ventral side of specimens from (a) Namibian site 26 (see Foissner et al. 2002a; 60 µm), (b) Austria (65 µm), (c) Brazil (71 µm), (d) Namibian site 31 (see Foissner et al. 2002a; 60 µm), (e) Saudi Arabia (78 µm), and (f) Venezuela (79 µm). Note the variability of the cirral pattern. Page 68.

tal cirri form transverse pseudorow; according to the illustration, however, they are not distinctly larger than the remaining cirri. Buccal cirrus right of anterior portion of paroral. One cirrus (III/2) behind right frontal cirrus. Five frontoventral cirri form slightly oblique row (likely a mixed row) extending from near anterior end of right marginal row to level of buccal cirrus. One pretransverse ventral cirrus and four transverse cirri which protrude distinctly beyond rear cell end. Right marginal row commences at 13% of body length, composed of 21 cirri. Left marginal row begins behind buccal vertex, made up of 10 cirri only in specimen illustrated. Both marginal rows slightly shortened posteriorly. Dorsal bristles "long", arranged in four "complete" (= bipolar) kineties; length of bristles and exact arrangement of kineties not described. Gap between marginal rows occupied by four conspicuous caudal cirri which are about twice as along as the marginal cirri.

Gonostomum ciliophorum Gellért, 1956a (Fig. 118h in Berger 1999): See also first sentence at *G. spirotrichoides*. Body length 70 µm; body length:width ratio of specimen illustrated 3.2:1. Body shape constantly narrow. Two ellipsoidal macronuclear nodules slightly left of midline, each one in anterior and posterior body half; one micronucleus per macronuclear nodule. Contractile vacuole at level of buccal vertex near left body margin; contracts every 6–7 s. Cytoplasm bright, translucent. Presence/absence of cortical granules not mentioned. Adoral zone gonostomatid, occupies 50% of body length, composed of 30–32 membranelles; similar as in *G. bryonicolum*, the major part of the marginally running membranelles are laterally arranged. Buccal lip rather large and obviously distinctly convex, covers moderately large buccal field. Paroral composed of about 10 widely spaced cilia in specimen illustrated; extends from near buccal vertex to near buccal cirrus (note that details must not be overinterpreted). Cytopharynx extends obliquely backwards. Specimen illustrated with 17 frontal-ventral-transverse cirri, that is, 18-cirri pattern almost complete: three "distinct" frontal cirri, but according to the illustration they are not markedly stronger than the other frontal-ventral- transverse cirri; left cirrus only inconspicuously displaced posteriad. Buccal cirrus slightly ahead of paroral. Four frontoventral cirri and three postoral ventral cirri with rear-

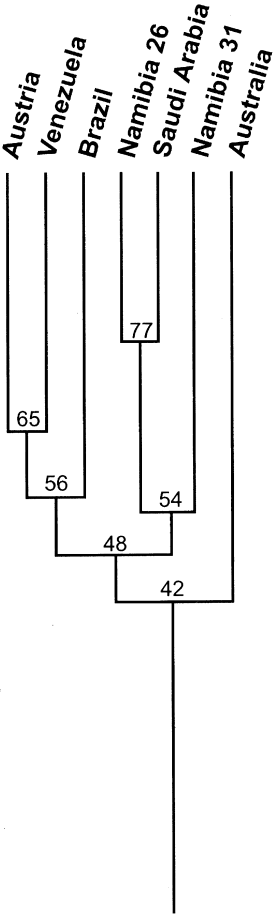


Fig. 13a *Gonostomum affine* ("Austria" to "Namibia 31") and *G. strenuum* from Australia (from Foissner et al. 2001). Similarity tree based both on morphological data and RAPD-fingerprint analyses. *Gonostomum strenuum* is clearly separated from *G. affine*. Further details, see text. Page 68.

most cirrus (V/3) distinctly ahead of level of buccal vertex. Two pretransverse ventral cirri and four prominent transverse cirri, the two rightmost being longer than the two leftmost and protrude distinctly beyond rear body end; only one transverse cirrus (II/1?) lacking. Right marginal row commences at 11% of body length, extends to rear cell end and therefore not separated from rear end of left marginal row, which begins at level of buccal vertex; right row composed of about 24 cirri, left of about 14 cirri. No information (length and arrangement of dorsal bristles; caudal cirri present/absent) provided about dorsal infraciliature.

Gonostomum geleii Gellért, 1957 (Fig. 118b in Berger 1999): The original description is in Hungarian and therefore I got most data from the illustration. Likely, the description is based – as in other descriptions provided by Gellért – on a single specimen only. Body length about 50 µm; body length:width ratio of specimen illustrated 2.9:1. Body outline roughly spindle-shaped, that is, widest in mid-body and rather narrowly rounded at both ends. Macronuclear nodules ellipsoidal, slightly left of midline, one in anterior and one in posterior body half; one globular micronucleus per macronuclear nodule. Contractile vacuole close to buccal vertex and left cell margin. Presence/absence of cortical granules very likely not described. Adoral zone gonostomatid, very prominent, occupies 50% of body length, composed of 17 membranelles. Paroral composed of about 16 rather widely spaced cilia, extends from buccal vertex to level of buccal cirrus (details must not be overinterpreted). Buccal field obviously very small. Specimen illustrated with only 11 frontal-ventral-transverse cirri, namely, three frontal cirri with left cirrus somewhat displaced posteriad; one buccal cirrus at level of anterior end of undulating membrane; three frontoventral cirri; and four transverse cirri protruding far beyond rear cell end. Right marginal row composed of 11 cirri, distinctly shortened anteriorly; left row composed of seven cirri only; rows distinctly separated posteriorly. Likely no information provided about dorsal infraciliature (length and arrangement of dorsal bristles; caudal cirri present/absent).

Trachelostyla canadensis Buitkamp & Wilbert, 1974 (Fig. 117p in Berger 1999): Body length 63–80 µm (method, in life or protargol impregnation, not indicated); length:width ratio of specimen illustrated 2.6:1. Body outline elliptical with both ends more or less broadly rounded. Two macronuclear nodules slightly left of midline, each one in anterior and posterior body half; length:width ratio of individual nodules 2:1; each nodule with one micronucleus. Contractile vacuole behind buccal vertex, that is, slightly displaced inwards. Presence/absence of cortical granules and cytoplasmic inclusions not described. Movement moderately fast, jerky, due to breaks for food-uptake; when freely swimming it rotates about main body axis. Adoral zone gonostomatid, prominent because occupying about 50% of body length, composed of 22 membranelles in specimen illustrated. Distalmost membranelles strong, about 16 µm long. Buccal lip about 7–9 µm long. Undulating membranes not illustrated in detail; the row illustrated is composed of about 30 basal bodies indicating that it is the endoral. Pharyngeal fibres extend obliquely backwards. Usually 10 "enlarged" frontoventral cirri (however, according to the illustration their bases are

not larger than that of the marginal cirri). Three frontal cirri, about 12 µm long, left one slightly displaced posteriad. Buccal cirrus distinctly ahead of undulating membrane. Six frontoventral cirri forming two rows with three cirri each, that is, one cirrus less than the full set of seven cirri (four frontoventral plus three "postoral"); invariably two frontoterminal cirri close to anterior end of right marginal row. Two relatively short (10 µm) transverse cirri. Right marginal row commences at level of frontoterminal cirri, composed of 21–23 cirri, ends – like left row – about at level of transverse cirri. Left marginal row commences close to buccal vertex, composed of 13–14 cirri; marginal cirri 9 µm long. Dorsal bristles 3 µm long, arranged in four kineties; three of them with each one caudal cirrus (variability of this pattern not described).

Gonostomum singhii Kamra, Kumar & Sapra, 2008 (Fig. 14d–f, Table 14): Kamra et al. (2008) did not make an illustration of a live specimen, but provided a micrograph showing mainly the body outline and the gonostomatid adoral zone. Body size of live specimens 71 × 26 µm on average. Invariably two ellipsoidal macronuclear nodules, each with one spherical micronucleus. Contractile vacuole at level of buccal vertex near left body margin. Cortical granules colourless, do not stain with protargol and not arranged in a distinct order; size and shape not indicated. Adoral zone gonostomatid, occupies 50% of body length, consists of 27 membranelles on average. Paroral composed of 14–16 widely spaced (distance 0.8 µm) cilia, form slightly curved row occupying about 16% of body length. Endoral composed of narrowly spaced cilia; anterior end about at mid-region of paroral. Cirral pattern very constant (Fig. 14d, Table 14): three frontal cirri in gonostomatid arrangement; buccal cirrus right of anterior end of paroral; four frontoventral cirri with the two frontoterminal cirri at anterior end of right marginal row; three postoral ventral cirri about at level of paroral; two rather small pretransverse ventral cirri; four transverse cirri. Right marginal row slightly shortened anteriorly and posteriorly. Left row commences at level of buccal vertex, terminates at about same level as right row, that is, marginal rows distinctly separated posteriorly. According to the original description, the cirri of *G. singhii* are very long and hypertrophied, a feature also described for *G. ciliophorum* (see remarks): frontal and transverse cirri 16–18 µm long; frontoventral, postoral ventral, marginal, and caudal cirri 10–13 µm; pretransverse ventral cirri 10–11 µm, distinctly thinner than transverse cirri. Dorsal bristles 2–3 µm long, arranged in three bipolar dorsal kineties; each kinety with a single caudal cirrus.

Foissner et al. (2001) compared six populations of *G. affine* from Europe, Africa, and South America (details on sample sites see occurrence) using morphological features and RAPD-fingerprints (Fig. 12a–f, Table 14). The morpho-trees did not agree with the RAPD-trees and both did not show a distinct biogeographical pattern. Even a tree based on both methods did not provide a clear pattern, indicating that the studied *G. affine*-like morphotypes fall into the range of natural variability of a single species (Fig. 13a).

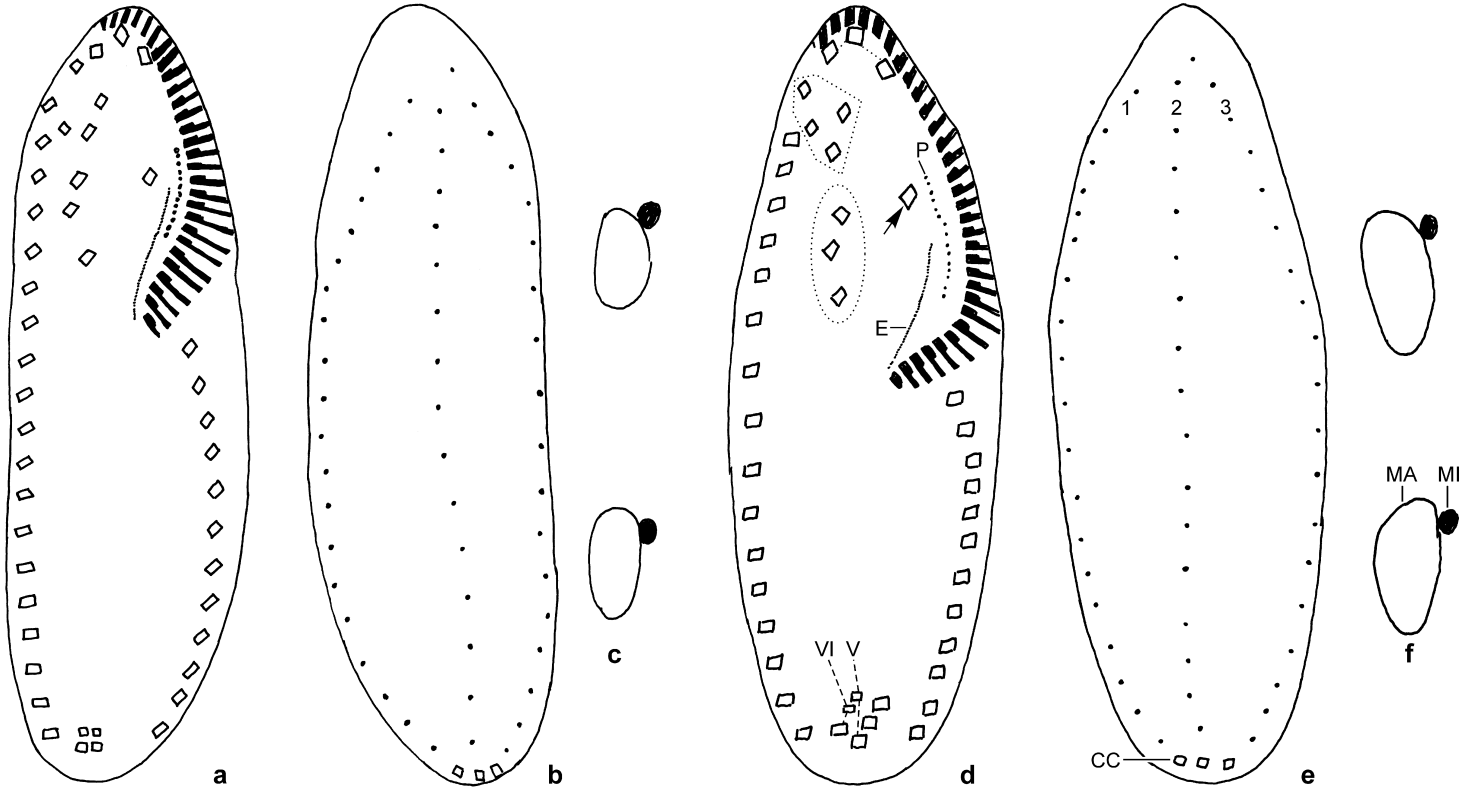


Fig. 14a–f *Gonostomum affine* (after Kamra et al. 2008. Protargol impregnation). **a–c:** Infraciliature of ventral and dorsal side and nuclear apparatus, 58 µm. **d–f:** Infraciliature of ventral and dorsal side and nuclear apparatus of the new synonym *G. singhii*, 68 µm. There is no "significant" difference to *G. affine*, so that the validity of *G. singhii* is not supported. Arrow marks buccal cirrus, polygon encloses the frontoventral cirri. The ellipse encloses the postoral ventral cirri which are not behind the adoral zone, as in many other 18-cirri hypotrichs, but right of the adoral zone. Frontal cirri connected by dotted line. CC = caudal cirri, E = endoral, MA = macronuclear nodule, MI = micronucleus, P = paroral, V, VI = frontal-ventral-transverse cirri anlagen (only shown in posterior portion), 1–3 = dorsal kineties. Page 68.

The population described by Dragesco (2003) from Rwandese soil agrees very well with the other "typical" *G. affine* populations. Thus, the reader is referred to the illustrations and the morphometric characterisation (Fig. 10i–m, Table 14).

Gonostomum algicola sensu Kim & Shin (2006, Fig. 14g–k, Table 14) agrees very well with *G. affine*. Thus, the reader is mainly referred to the illustrations and Table 14). They measured the "length of the undulating membranes", but provided no explanation; likely this is the distance between the anterior end of the paroral and the posterior end of the endoral (mean = 27.2; SD = 4.1; Min = 21; Max = 35; n = 25). Contractile vacuole 10–15 µm across, during diastole with long collecting canals and split into three small vacuoles. Cortical granules colourless, irregularly distributed on dorsal surface.

Gonostomum sp. 2 of Shin (1994, Fig. 14l–n; Table 14) is relatively large, namely, 80–130 × 30–65 µm. Body soft, flexible. Contractile vacuole about at midbody near left cell margin; movement rapid. Adoral zone occupies about 46% of body length. "Length of undulating membranes" 23.8 µm on average (range 21–26 µm; n = 20; no explanation given, likely it is the distance between the anterior end of the paroral and the rear end of the endoral). Shin likely confused endoral and paroral because according to his Table 16 the paroral is on average 16 µm (range 12–24 µm) long, the endoral only 13 µm (range 11–16 µm); by contrast, in Fig. 14m the paroral is, as is usual for *Gonostomum*, shorter than the endoral. Pharyngeal fibres 10–25 µm long. Invariably one buccal cirrus, which is, however, not illustrated (Fig. 14l, m). Usually five (4–6) frontoventral cirri (frontoterminal cirri included) on frontal area (Fig. 14m), that is, two cirri less than in the ordinary *Gonostomum* pattern (Fig. 3a). Kinety 2 composed of about 15 dikinetids. Dorsal bristles up to 5 µm long.

Cell division (Fig. 11b–j, Table 15): The cell division described by Hemberger (1982) was reviewed by Berger (1999, Fig. 120a–j in this book). Eigner (1999) studied the cell division of *G. affine* and *G. kuehnelti* and found only one major difference, namely in the development of anlage I. In the present species anlage I is formed independently in proter (from parental paroral) and opisthe (from oral primordium). In *G. kuehnelti* anlage I of both daughter cells shall be formed from a very long primary primordium, an observation which should be checked in a second population. Further details, see *G. kuehnelti* and *G. algicola*.

Stein (1859) found an early to middle divider already clearly showing the new adoral zone and the biscuit-shaped macronucleus (Fig. 10e).

Conjugation (Fig. 10c, f; Fig. 117q in Berger 1999): Stein (1859) described and illustrated two stages of conjugation, still interpreted as "longitudinal division" at that time. The two specimens unite, as is usual, anteriorly; specimens rectangularly arranged, that is, when right specimen shows ventral side then the left lateral side of the left specimen is recognisable (Fig. 10c). Postconjugates very slender and almost with parallel cell margins (Fig. 10f), a feature confirmed by Buitkamp (1977; Fig. 117q in Berger 1999).

Occurrence and ecology: *Gonostomum affine* is certainly the most widely distributed and most common, and often also the most abundant hypotrich in almost all

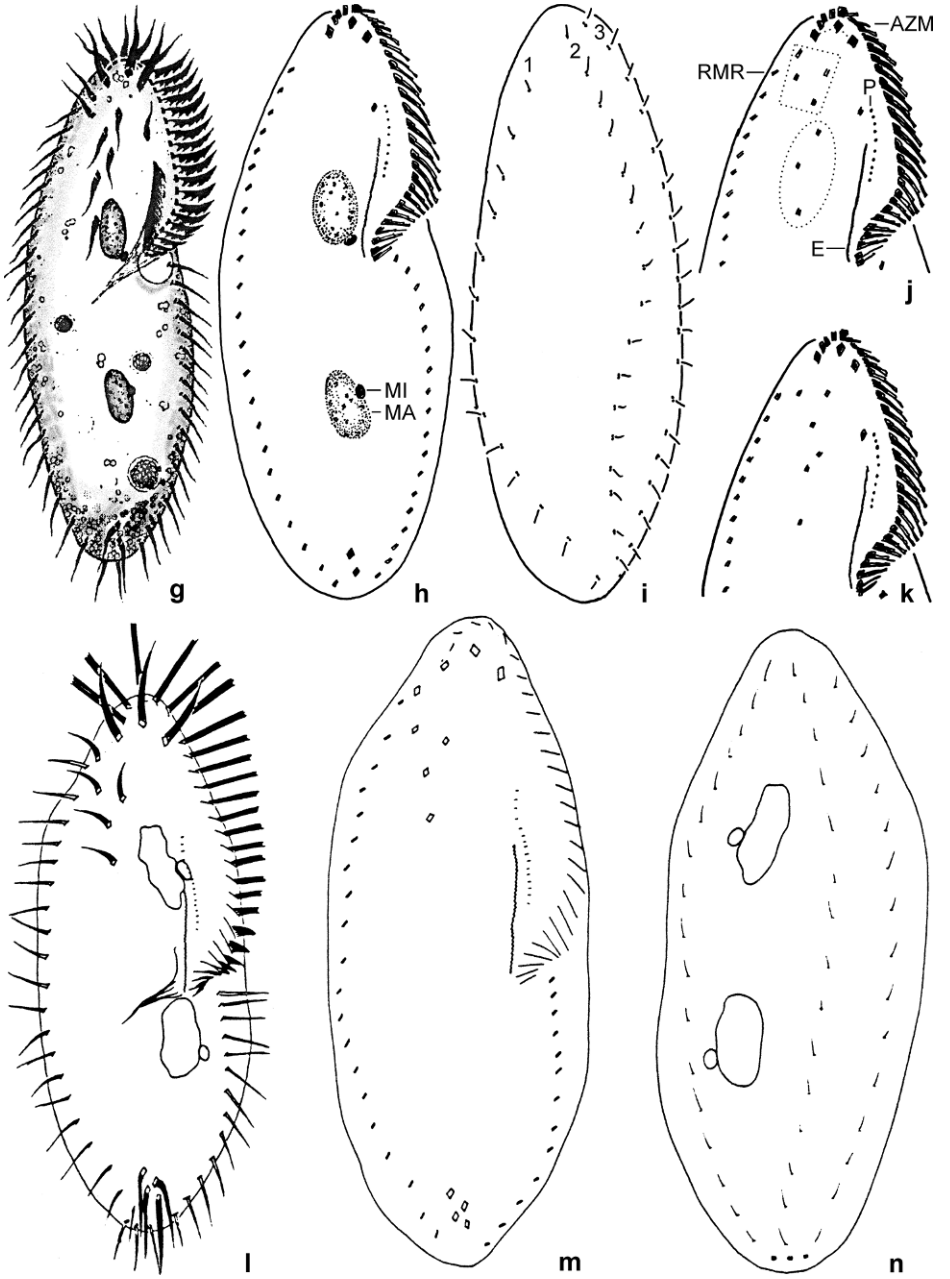


Fig. 14g–n *Gonostomum affine* (g–k, after Kim & Shin 2006; l–n, from Shin 1994. g, l, from life; h–k, m, n, protargol impregnation). **g, l:** Ventral views, g = 98 µm, l = 106 µm. **h–k:** Infraciliature of ventral (h, j, k) and dorsal side (i), h, i = 98 µm. Note that the paroral is made up of 10 cilia, indicating that this is *G. affine*, and not *G. algicola*, as incorrectly assumed by Kim & Shin (2006). In (h) the frontoventral cirri are not illustrated (see [j, k] for variability). Postoral ventral cirri encircled; frontoventral cirri (III/2, IV/3, VI/3, VI/4) surrounded by polygon; frontal cirri connected by dotted line. Note that the caudal cirri at the end of the dorsal kineties are not illustrated in (i). **m, n:** Infraciliature of ventral and dorsal side (of same

terrestrial habitats (e.g., soil, litter, moss, lichens) from all over the world (for reviews, see Foissner 1998, Berger 1999). However, it also occurs in limnetic habitats, especially when edaphic influence, for example, after flooding, is present, or when high amounts of decaying leave litter are available (Foissner & Berger 1996, p. 471). In the aufwuchs and sediment of large brooks, rivers, and lakes of Austria, however, *Gonostomum affine* is very rare (e.g., AOÖLR 1997, determination H. Blatterer; own observations). The locus classicus, that is, the sample site of the type population of *Gonostomum affine* is the "St. Procop-Thal" (new, common spellings: Procop-Tal, Prokop-Tal, Prokoptal, St. Prokop-Tal, Prokopské údolí, Prokop Valley) in the south-western suburbs of the city of Prague, Czech Republic (Stein 1859). Stein separated this species for the first time from *Oxytricha pellionella* (now *Tachysoma pellionellum*; for review, see Berger 1999, p. 433) in early March 1857. He found it in high abundance in water (type [pond, brook, ...] not mentioned) where fallen leaves of trees moulded and many larvae of phryganids (Trichoptera) lived, indicating that Stein collected the sample in a more or less permanent water body with distinct edaphic influence. Later, he found it also very often in marshy waters in the "Baumgarten" (Stromovka), an urban park in Prague, sometimes likewise simultaneously with *T. pellionellum*. It seems to be a discrepancy that the most common soil hypotrich was discovered in a limnetic habitat. However, one needs to know that at that time (roughly until the late 1800) basically no one looked after ciliates in terrestrial habitats (for review, see Foissner 1987a). So it is no wonder, that such a common species was not discovered earlier. By contrast, *Holosticha pullaster* – probably the most common hypotrich in limnetic habitats – was discovered by the early O. F. Müller (Müller 1773; for review, see Berger 2006a, p. 128). Interestingly, *H. pullaster* was also rather often (12 times!) described as new species so that one can assume that common species have distinctly more synonyms than rare.

The type locality of the synonym *G. spirotrichoides* is the south-western region of the hill Magoska north-east of the Hungarian village of Boldogkőváralja, where Gellért (1956a) discovered it in humus under moss on hypersthenaugitandesit rocks. Feeds on bacteria and debris. No further records published.

The type locality of *G. bryonicolum* is the same as for *G. spirotrichoides* (see there). Feeds on debris and ciliates (Gellért 1957, p. 15). The type locality of *G. ciliophorum* is the same as for *G. spirotrichoides* (see there). Feeds on debris and bacteria. No further records published.

Type locality of *G. geleii*: Gellért (1957) studied soil samples from various habitats in Hungary. Unfortunately, he did not name the individual localities in the German summary. According to Gellért (1957, Table 1) and Stiller (1974, p. 92), *Gonostomum geleii* was discovered in a soil sample from a coniferous forest also near the village of Boldogkőváralja. Feeds on algae. Note that *Urosoma macrostomum*, a

Continued on p. 103

← specimen?), 103 µm. AZM = adoral zone of membranelles, E = endoral, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = right marginal row, 1–3 = dorsal kineties. Page 68.

Table 14 Morphometric data on *Gonostomum affine* (af1, Rwandan population from Dragesco 2003; af2, Austrian population from Foissner et al. 2001; af3, Saudi Arabian population from Foissner et al. 2001; af4, Namibian site 26 population from Foissner et al. 2001; af5, Namibian site 31 population from Foissner et al. 2001; af6, Venezuelan population from Foissner et al. 2001; af7, Brazilian population from Foissner et al. 2001; af8, *G. algicola* of Kim & Shin 2006; af9, *Gonostomum* sp. 2 from Shin 1994), *Gonostomum albicarpathicum* (alb, from Vd'ačný & Tirjaková 2006), *Gonostomum algicola* (alg, from Foissner et al. 2002a), *Gonostomum gonostomoidum* (go1, type population from Hemberger 1982, 1985 [sample size not clearly indicated]; go2, Korean population from Kim & Shin 2006; go3, Indian population from Kamra et al. 2008), *Gonostomum kuehnelti* (ku1, from Foissner 1987c; ku2, from Eigner 1999; ku3, from Kamra et al. 2008), *Gonostomum namibiense* (na1, type population; na2, population from site 30; both from Foissner et al. 2002a), *Gonostomum singhii*, a new synonym of *G. affine* (sin, from Kamra et al. 2008), *Gonostomum* sp. 1 (sp1, from Shin 1994), *Gonostomum strenuum* (st1, Australian population from Foissner et al. 2001; st2, neotype population from Foissner et al. 2002a; st3, Spanish population from Olmo & Téllez 1997; st4, Venezuelan *G. affine* population from Foissner 2000; st5, Chinese population from Song 1990)

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	af1	97.0	95.0	11.4	3.3	11.0	76.0	113.0	12
	af2	79.0	80.0	11.6	2.5	14.7	63.0	100.0	21
	af3	68.8	68.0	9.4	2.1	13.7	50.0	85.0	21
	af4	60.5	62.0	7.3	1.6	12.1	50.0	75.0	21
	af5	75.8	74.0	7.2	1.6	9.5	67.0	97.0	21
	af6	72.5	71.0	6.0	1.3	8.3	60.0	82.0	21
	af7	81.0	82.0	8.7	1.9	10.8	70.0	93.0	21
	af8[p]	101.1	102.0	6.9	1.4	6.8	88.0	113.0	25
	af8	91.6	91.0	6.6	1.3	7.2	78.0	108.0	25
	af9	103.8	108.0	12.9	2.9	12.4	79.0	120.0	20
	alb	65.6	64.1	10.9	3.5	16.6	53.1	89.1	10
	alg	71.2	70.0	10.7	2.5	15.0	52.0	95.0	19
	go1	–	–	–	–	–	110.0	200.0	>50
	go2[p]	86.8	88.0	14.2	3.3	16.3	60.0	121.0	19
	go2	106.5	108.0	11.3	3.6	10.6	85.0	124.0	10
	go3	78.0	–	–	–	–	–	–	?
	ku1	60.2	58.0	6.6	1.7	10.9	50.0	71.0	15
	ku3	61.6	–	5.2	–	8.4	55.2	70.0	10
	na1	72.9	73.0	6.8	1.6	9.4	60.0	85.0	18
	na2	100.2	102.0	9.2	2.0	9.2	84.0	115.0	21
	sin	66.2	–	4.9	–	7.4	60.8	76.3	10
	sp1	129.8	132.0	17.6	3.5	13.5	87.0	155.0	25
	st1	93.9	94.0	10.6	2.3	11.2	75.0	112.0	21
	st2	81.5	80.0	7.8	2.2	9.6	72.0	98.0	13
	st3	124.9	120.0	9.8	–	7.9	110.0	145.0	30
	st4	81.0	80.0	9.8	2.1	12.1	67.0	100.0	21
	st5	103.8	–	7.9	2.4	7.6	88.0	119	11
Body, width	af1	28.0	28.0	2.2	0.6	8.0	24.0	32.0	12
	af2	34.7	33.0	5.3	1.2	15.4	28.0	44.0	21
	af3	28.6	30.0	4.1	0.9	14.2	21.0	35.0	21
	af4	29.2	29.0	4.5	1.0	15.6	21.0	37.0	21
	af5	31.8	31.0	3.8	0.8	12.0	26.0	40.0	21
	af6	29.9	32.0	5.4	1.2	18.0	20.0	40.0	21
	af7	32.8	33.0	5.1	1.1	15.5	24.0	41.0	21
	af8[p]	35.0	35.0	3.5	0.7	10.0	30.0	40.0	25
	af8	37.6	39.0	5.2	1.0	13.8	26.0	45.0	25

Table 14 Continued

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, width	af9	47.7	47.5	10.6	2.4	22.2	30.0	65.0	20
	alb	20.3	20.3	3.9	1.2	19.0	15.0	28.1	10
	alg	18.9	19.0	3.8	0.9	19.9	14.0	27.0	19
	go1	–	–	–	–	–	30.0	50.0	>50
	go2[p]	29.8	30.0	4.0	1.0	14.8	21.0	40.0	19
	go2	44.1	46.0	8.7	7.8	19.7	30.0	55.0	10
	go3	23.0	–	–	–	–	–	–	?
	ku1	23.7	24.0	2.7	0.7	11.6	20.0	28.0	15
	ku3	18.6	–	3.3	–	17.8	15.3	26.4	10
	na1	23.4	23.5	2.0	0.5	8.7	20.0	28.0	18
	na2	27.0	27.0	4.8	1.1	17.6	19.0	36.0	18
	sin	22.8	–	2.6	–	11.3	18.0	27.0	10
	sp1	48.2	48.0	9.4	1.9	19.4	30.0	64.0	25
	st1	38.3	37.0	4.8	1.0	12.4	32.0	48.0	21
	st2	30.0	30.0	2.9	0.8	9.6	26.0	36.0	13
	st3	51.4	50.5	6.4	–	12.5	40.0	65.0	30
	st4	30.1	30.0	3.6	0.8	12.1	22.0	35.0	21
	st5	37.0	–	5.0	1.5	13.4	28.0	44.0	11
Body length:width, ratio	af8[p]	2.9	2.9	0.2	0.0	6.6	2.6	3.3	25
	af8	2.5	2.4	0.4	0.1	15.9	2.0	3.3	25
	af9	2.2	2.2	0.4	0.1	16.8	1.7	3.1	20
	alb	3.3	3.2	0.3	0.1	8.4	2.9	3.6	10
	alg	3.9	3.7	0.9	0.2	22.6	2.6	5.9	19
	go1	–	–	–	–	–	3.0	.0	>50
	go2[p]	3.0	3.0	0.6	0.1	19.2	2.1	4.2	19
	go2	2.5	2.6	0.4	0.1	15.5	1.8	3.0	10
	ku3	3.3	–	0.5	–	14.7	2.5	4.1	10
	na1	3.1	3.0	0.4	0.1	12.5	2.7	4.3	16
	na2	3.8	3.6	0.6	0.1	14.9	2.9	5.0	18
	sin	2.9	–	0.3	–	11.8	2.3	3.5	10
	sp1	2.8	2.7	0.5	0.1	19.3	2.1	4.0	25
	st2	2.7	2.8	0.3	0.1	10.3	2.3	3.5	13
Adoral zone of membranelles, length	af1	48.0	48.0	5.5	1.6	7.0	41.0	58.0	12
	af2	41.9	43.0	7.6	1.7	18.0	29.0	55.0	21
	af3	33.2	34.0	4.1	0.9	12.4	26.0	40.0	21
	af4	29.2	29.0	3.7	0.8	12.5	25.0	42.0	21
	af5	36.6	37.0	1.5	0.3	4.1	34.0	40.0	21
	af6	33.2	33.0	2.9	0.6	8.7	29.0	38.0	21
	af7	39.2	39.0	1.9	0.4	4.9	36.0	44.0	21
	af8[p]	38.6	38.0	5.9	1.2	15.4	30.0	49.0	25
	af8	39.9	40.0	2.2	0.4	5.6	35.0	44.0	25
	af9	48.1	50.0	3.9	0.9	8.2	40.0	56.0	20
	alb	27.6	26.0	4.5	1.4	16.5	23.1	35.2	10
	alg	16.6	26.0	2.1	0.5	7.8	24.0	31.0	19
	go2[p]	42.5	40.0	7.3	1.7	17.1	30.0	58.0	19
	go2	54.1	54.0	2.7	0.9	5.0	50.0	58.0	10
	ku1	28.0	28.0	1.5	0.4	5.4	25.0	32.0	15
	ku3	29.2	–	1.6	–	5.5	26.5	31.6	10
	na1	28.7	28.5	2.3	0.5	8.0	24.0	32.0	18
	na2	40.8	40.0[c]	4.9	1.1	12.1	29.0	52.0	21

Table 14 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Adoral zone of membranelles, length	sin	32.5	–	2.3	–	7.0	29.0	35.7	10
	sp1	67.6	70.0	9.0	1.8	13.3	45.0	80.0	25
	st1	44.5	44.0	2.7	0.6	6.0	40.0	50.0	21
	st2	42.3	43.0	4.9	1.4	11.6	32.0	49.0	13
	st3	58.6	60.0	2.5	–	4.3	55.0	65.0	30
	st4	33.9	33.0	2.7	0.6	7.8	30.0	39.0	21
	st5	54.5	–	7.2	2.2	13.2	41.0	69.0	11
Paroral, length	alb	6.5	6.6	0.6	0.2	8.9	5.5	7.0	10
	alg	2.9	3.0	1.0	0.2	34.3	1.0	4.0	19
	ku3	5.4	–	0.2	–	3.4	4.9	5.5	10
	na1	5.6	6.0	1.0	0.3	18.2	4.0	7.0	14
	na2	9.4	9.0	1.3	0.3	14.2	6.0	12.0	18
	sin	10.6	–	0.3	–	2.5	10.1	11.2	10
	st2	8.1	8.0	1.4	0.4	17.8	6.0	10.0	13
	st3 [q]	14.6	–	–	–	–	–	–	1
Endoral, length	alb	10.1	9.4	3.4	1.1	33.6	7.8	18.0	10
	alg	10.9	11.0	0.7	0.2	6.8	10.0	12.0	19
	go2	21.7	22.0	1.6	0.5	7.2	18.0	23.0	10
	na1	10.8	11.0	1.3	0.3	12.2	8.0	12.0	15
	na2	12.6	13.0	2.0	0.5	16.1	7.0	14.0	18
	st2	14.8	15.0	1.1	0.3	7.4	12.0	16.0	13
Body length:length of adoral zone, ratio	af8 [p]	2.7	2.6	0.4	0.1	13.3	2.2	3.3	25
	af8	2.3	2.3	0.2	0.0	8.8	2.0	2.8	25
	af9	2.2	2.2	0.2	0.1	9.8	1.8	2.6	20
	alb	2.4	2.5	0.2	0.1	9.8	2.0	2.7	10
	alg	2.7	2.7	0.3	0.1	12.7	2.1	3.4	19
	go1	–	–	–	–	–	2.0	3.0	>50
	go2 [p]	2.1	2.1	0.2	0.0	9.6	1.8	2.6	19
	go2	2.0	1.9	0.2	0.1	9.0	1.6	2.2	10
	na1	2.5	2.6	0.2	0.1	9.0	2.1	2.9	18
	na2	2.5	2.5	0.3	0.1	12.3	1.7	3.2	21
	sp1	1.9	1.9	0.1	0.0	7.0	1.7	2.3	25
	st2	1.9	1.9	0.2	0.1	9.5	1.7	2.3	13
Length of adoral zone:body length, ratio	go3 [l]	50.0	–	–	–	–	–	–	?
	ku3 [l]	47.6	–	4.5	–	9.4	40.5	52.8	10
	sin [l]	49.2	–	4.2	–	8.6	40.5	56.3	10
Anterior body end to paroral, distance	ku3	15.3	–	0.8	–	5.1	14.3	17.2	10
	sin	17.1	–	1.3	–	7.8	14.6	20.0	10
	st2	23.8	25.0	3.1	0.9	13.0	17.0	27.0	13
Anterior body end to endoral, distance	ku3	17.6	–	0.7	–	3.9	17.0	19.1	10
	sin	22.9	–	1.5	–	6.7	20.3	25.6	10
	st2	27.3	28.0	3.7	1.0	13.7	20.0	32.0	13
Anterior body end to left frontal cirrus, distance	st2	5.2	5.0	0.7	0.2	13.9	4.0	6.0	13
Anterior body end to buccal cirrus, distance	na1	15.1	15.0	2.3	0.5	15.0	11.0	21.0	18
	na2	21.8	22.0	2.5	0.6	11.2	15.0	26.0	18
	st2	23.7	25.0	3.2	0.9	13.5	17.0	26.0	13
Anterior body end to frontoventral row III, distance [d]	st2	7.3	7.0	1.1	0.3	15.2	6.0	9.0	13
Anterior body end to end of frontoventral row III, distance [d]	st2	15.8	16.0	2.2	0.6	14.2	11.0	19.0	13

Table 14 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Anterior body end to frontoventral row IV, distance[d]	st2	10.1	10.0	1.3	0.3	12.5	7.0	12.0	13
Anterior body end to end of frontoventral row IV, distance[d]	st2	24.5	25.0	4.1	1.1	16.8	15.0	29.0	13
Anterior body end to frontoventral row V, distance[d]	st2	19.2	19.0	2.0	0.6	10.4	16.0	22.0	13
Anterior body end to end of frontoventral row V, distance[d]	st2	50.2	50.0	5.6	1.5	11.1	41.0	62.0	13
	st4	34.5	35.0	4.3	1.0	12.6	29.0	43.0	21
Anterior body end to end of frontoterminal cirri, distance[d]	st2	18.2	18.0	3.4	0.9	18.5	12.0	24.0	13
Anterior body end to last frontoventral cirrus, distance	af2	33.6	33.0	7.3	1.6	21.6	22.0	49.0	21
	af3	25.9	26.0	3.2	0.7	12.3	21.0	32.0	21
	af4	17.6	17.0	3.3	0.7	18.6	13.0	28.0	21
	af5	21.7	22.0	2.1	0.5	9.7	18.0	25.0	21
	af6	26.5	26.0	2.6	0.6	9.9	21.0	30.0	21
	af7	26.2	26.0	2.8	0.6	10.8	19.0	32.0	21
	alb	24.7	25.8	6.9	2.2	27.9	12.5	32.0	10
	alg	21.8	21.0	4.8	1.1	22.1	14.0	32.0	19
	na1	22.6	22.0	2.0	0.5	8.9	20.0	26.0	18
	na2	38.3	37.0	5.1	1.1	13.3	32.0	57.0	21
	st1	49.5	49.0	6.3	1.4	12.7	41.0	65.0	21
Anterior body end to anteriormost transverse cirrus, distance	na1	54.2	55.0	5.3	1.3	9.8	43.0	65.0	18
	na2	72.7	73.0	8.0	1.8	11.0	60.0	90.0	19
Posterior body end to transverse cirri, distance	st2	3.4	3.0	0.9	0.3	26.6	2.0	5.0	13
Anterior body end to anterior end of right marginal row, distance	na1	5.3	5.5	1.5	0.4	28.0	3.0	9.0	18
	na2	9.1	9.0	1.9	0.4	20.7	6.0	13.0	19
	st2	7.2	6.0	3.0	0.8	41.9	4.0	16.0	13
Posterior body end to right marginal row, distance	st2	4.0	4.0	1.4	0.4	35.1	2.0	6.0	13
Posterior body end to left marginal row, distance	st2	1.1	1.5	–	–	–	0.0	2.0	13
Anterior body end to dorsal kinety 1, distance	st2	13.4	14.0	2.3	0.6	16.9	10.0	16.0	13
Anterior body end to dorsal kinety 2, distance	st2	8.8	10.0	1.7	0.5	19.8	6.0	11.0	13
Anterior body end to dorsal kinety 3, distance	st2	5.3	6.0	0.9	0.3	17.8	3.0	6.0	13
Anterior body end to anterior macronuclear nodule, distance	st2	18.9	19.0	2.8	0.8	14.9	15.0	26.0	13
Anterior macronuclear nodule, length	af1 [i]	15.0	15.5	2.1	0.6	8.0	12.0	18.0	12
	af2	17.1	18.0	3.3	0.7	19.2	11.0	22.0	21
	af3	14.0	13.0	3.2	0.7	23.1	10.0	20.0	21
	af4	11.4	12.0	1.7	0.4	14.5	9.0	15.0	21
	af5	14.1	14.0	2.3	0.5	16.0	10.0	18.0	21
	af6	13.1	13.0	2.2	0.5	16.5	9.0	17.0	21
	af7	14.0	14.0	2.2	0.5	15.3	11.0	19.0	21
	af8	11.6	10.0	4.2	0.8	36.4	7.0	20.0	25
	af9 [i]	23.4	26.0	6.2	1.4	26.7	12.0	30.0	20
	alb	9.8	10.2	2.3	0.7	23.4	6.3	12.5	10

Table 14 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Anterior macronuclear nodule, length	alg	12.1	12.0	2.4	0.5	19.6	7.0	16.0	19
	go2	12.1	13.0	3.1	1.0	25.7	8.0	16.0	10
	go3 [i]	15.5	–	–	–	–	–	–	?
	ku1 [i]	4.5	4.0	1.1	0.3	25.3	3.0	7.0	15
	ku3 [i]	4.0	–	0.4	–	10.0	3.4	4.6	10
	na1	11.7	12.0	2.1	0.5	18.0	8.0	16.0	18
	na2	16.0	16.0	2.1	0.4	12.9	12.0	20.0	21
	sin [i]	10.6	–	1.3	–	12.1	8.6	12.9	10
	sp1	18.4	18.0	2.8	0.6	15.1	14.0	27.0	25
	st1	16.7	17.0	2.9	0.6	17.5	13.0	25.0	21
	st2	16.7	17.0	1.8	0.5	10.5	14.0	20.0	13
	st3 [i]	38.9	40.0	4.2	–	10.9	3.0	50.0	30
	st4 [i]	15.9	15.0	2.5	0.5	15.5	13.0	23.0	21
	st5 [i]	17.1	–	2.3	0.6	13.4	13.0	20.0	16
Anterior macronuclear nodule, width	af2	7.9	8.0	0.9	0.2	11.2	6.0	10.0	21
	af3	7.1	7.0	1.1	0.2	14.9	5.0	9.0	21
	af4	6.6	6.0	0.7	0.1	10.3	6.0	8.0	21
	af5	6.8	7.0	0.9	0.2	13.1	5.0	9.0	21
	af6	7.9	8.0	0.9	0.2	10.9	6.0	10.0	21
	af7	7.7	8.0	1.2	0.3	16.2	6.0	12.0	21
	af8	8.0	8.0	1.1	0.2	14.1	6.0	11.0	25
	af9 [i]	10.3	10.0	2.8	0.6	26.9	6.5	16.0	20
	alb	5.0	4.7	0.8	0.3	16.5	3.9	6.6	10
	alg	4.8	5.0	0.5	0.1	11.2	4.0	6.0	19
	go2	7.9	8.0	1.0	0.3	12.6	6.0	9.0	10
	go3 [i]	8.5	–	–	–	–	–	–	?
	ku1	3.8	4.0	0.7	0.2	17.1	3.0	5.0	15
	na1	5.3	6.0	1.0	0.2	18.2	4.0	6.0	18
	na2	5.4	6.0	0.7	0.1	12.5	4.0	6.0	21
	sin	5.8	–	0.9	–	15.0	4.5	7.0	10
	sp1	9.4	9.0	2.1	0.4	21.9	7.0	17.0	25
	st1	6.9	7.0	0.9	0.2	12.9	5.0	9.0	21
	st2	7.1	7.0	1.0	0.3	13.5	6.0	8.0	13
	st3 [i]	16.8	15.0	2.2	–	13.2	15.0	20.0	30
	st4 [i]	6.2	6.0	0.6	0.1	9.7	5.0	7.0	21
	st5 [i]	9.1	–	1.7	0.4	18.2	6.0	13.0	16
Posterior macronuclear nodule, length	af8	10.0	8.0	3.4	0.7	34.0	6.0	18.0	25
	go2	11.9	12.0	3.1	1.0	26.4	8.0	17.0	10
Posterior macronuclear nodule, width	af8	7.0	7.0	1.2	0.2	17.8	5.0	12.0	25
	go2	8.0	8.0	0.9	0.3	11.8	6.0	10.0	10
Macronuclear nodules, number	af2	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	af3	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	af4	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	af5	2.0	2.0	–	–	–	2.0	3.0	21
	af6	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	af7	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	af8	2.0	2.0	0.0	0.0	0.0	2.0	2.0	25
	af9	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	alb	4.3	4.0	1.2	0.4	27.4	3.0	6.0	10
	alg	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19

Table 14 Continued

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Macronuclear nodules, number	go1	2.0	–	–	–	–	2.0	2.0	>50
	go2	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
	go3	2.0	–	–	–	–	–	–	?
	ku1	14.2	15.0	2.1	0.5	14.9	10.0	17.0	15
	ku3	14.0	–	1.9	–	13.9	13.0	19.0	10
	na1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	18
	na2	2.0	2.0	–	–	–	2.0	2.0	21
	sin[m]	2.0	–	0.0	–	0.0	2.0	2.0	10
	sp1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	25
	st1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	st1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
	st3	2.0	2.0	0.0	–	0.0	2.0	2.0	30
	st4	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	st5	2.0	–	0.0	0.0	0.0	2.0	2.0	17
Macronuclear nodules in anterior group, number	ku3	6.5	–	1.0	–	14.9	6.0	9.0	10
Macronuclear nodules in posterior group, number	ku3	8.1	–	1.0	–	12.3	6.0	10.0	10
Nuclear figure, length	alb	36.2	35.9	6.6	2.1	18.1	28.1	48.4	10
	ku1	41.2	39.0	4.9	1.3	12.0	35.0	49.0	15
	st2	43.0	42.0	4.2	1.2	9.8	37.0	51.0	13
Macronuclear nodule pairs, distance in between	alb	5.9	5.1	3.9	1.2	66.9	0.0	12.5	10
Macronuclear nodules, distance in between	af8	21.6	21.0	2.6	0.5	11.8	18.0	27.0	25
	go2	28.0	25.0	10.0	3.2	35.6	13.0	48.0	10
	st2	11.2	10.0	3.2	0.9	28.7	7.0	28.0	13
Anterior micronucleus, diameter	af9[k]	2.7	2.5	0.6	0.2	22.9	2.0	4.0	18
	alb	2.3	2.3	0.6	27.4	0.2	1.6	3.3	10
	go2	2.5	2.0	0.5	0.2	21.1	2.0	3.0	10
	go3[k]	2.2	–	–	–	–	–	–	?
	ku3[k]	1.1	–	0.1	–	11.8	1.0	1.4	10
	sin[k]	2.0	–	0.3	–	13.3	1.4	2.4	10
	sp1[k]	2.3	2.5	0.3	0.1	11.0	2.0	2.5	22
	st3[k]	4.4	4.0	0.5	–	11.3	4.0	5.0	30
Anterior micronucleus, length	af2[k]	3.1	3.0	0.8	0.2	25.4	2.0	4.0	21
	af3[k]	2.3	2.5	0.3	0.1	15.0	2.0	3.0	21
	af4[k]	2.2	2.0	0.5	0.1	20.9	2.0	3.0	21
	af6[k]	2.1	2.0	0.3	0.1	13.0	1.0	3.0	21
	af7[k]	2.8	3.0	0.4	0.1	14.3	2.0	4.0	21
	af8[k]	2.1	2.0	0.3	0.1	15.6	2.0	3.0	25
	alg[k]	1.1	1.0	–	–	–	1.0	2.0	19
	na1	2.2	2.2	–	–	–	1.6	3.2	18
	na2	1.8	1.6	–	–	–	1.5	2.4	20
	st1	3.0	3.0	0.3	0.1	10.5	3.0	4.0	21
	st2	1.9	2.0	–	–	–	1.5	2.5	13
	st4[k]	2.9	3.0	–	–	–	3.0	4.0	21
	st5[k]	2.3	–	0.3	0.1	13.5	1.9	2.8	16
Anterior micronucleus, width	af2[k]	2.3	2.5	0.5	0.1	21.9	2.0	3.0	21
	af3[k]	1.9	2.0	0.2	0.1	12.4	2.0	3.0	21
	af4[k]	1.4	1.5	0.3	0.1	21.6	1.0	2.0	21

Table 14 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Anterior micronucleus, width	af6 [k]	1.9	2.0	0.2	0.1	12.7	1.0	2.0	21
	af7 [k]	2.0	2.0	0.2	0.0	11.2	2.0	3.0	21
	alg [k]	1.0	1.0	–	–	–	.0	1.0	19
	na1	2.0	2.0	–	–	–	1.6	2.4	18
	na2	1.7	1.6	–	–	–	1.6	2.5	20
	st1	2.3	2.0	0.3	0.1	13.5	2.0	3.0	21
	st2	1.9	2.0	–	–	–	1.5	2.5	13
	st4 [k]	2.0	2.0	–	–	–	2.0	3.0	21
Micronuclei, number	af2	1.9	2.0	0.6	0.1	30.9	0.0	3.0	21
	af3	2.3	2.0	1.0	0.2	44.1	0.0	4.0	21
	af4	1.9	2.0	0.4	0.1	22.9	1.0	3.0	21
	af5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21
	af6	1.9	2.0	1.0	0.2	51.9	0.0	4.0	21
	af7	1.7	2.0	0.6	0.1	32.7	0.0	2.0	21
	af8	2.2	2.0	0.4	0.1	17.3	2.0	3.0	25
	af9	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
	alb	2.4	2.0	0.7	0.2	31.3	2.0	4.0	10
	alg	1.6	2.0	–	–	–	.0	3.0	19
	go1	2.0	–	–	–	–	2.0	2.0	>50
	go2	3.1	3.0	1.4	0.4	44.2	1.0	6.0	10
	go3	–	–	–	–	–	3.0	4.0	?
	ku3	2.0	–	0.0	–	0.0	2.0	2.0	10
	na1	2.1	2.0	0.6	0.1	27.6	1.0	4.0	18
	na2	2.8	2.5	1.3	0.3	45.8	1.0	7.0	20
	sin	2.0	–	0.0	–	0.0	2.0	2.0	10
	sp1	1.9	2.0	0.6	0.1	30.1	1.0	3.0	22
	st1	3.1	3.0	1.3	0.3	40.6	0.0	6.0	21
	st2	4.6	5.0	1.5	0.4	32.5	3.0	8.0	13
	st3	3.5	4.0	0.9	–	26.5	2.0	5.0	30
	st4 [r]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	st5	2.1	–	0.3	0.1	15.7	2.0	3.0	17
Adoral membranelles, number	af1	31.0	31.0	2.2	0.6	14.0	27.0	36.0	12
	af2	28.8	30.0	4.2	0.9	14.6	23.0	35.0	21
	af3	21.5	22.0	2.2	0.5	10.4	17.0	24.0	21
	af4	22.0	22.0	2.0	0.4	9.2	18.0	27.0	21
	af5	25.9	26.0	1.0	0.2	3.8	24.0	28.0	21
	af6	24.7	25.0	1.6	0.4	6.6	21.0	27.0	21
	af7	27.1	27.0	0.9	0.2	3.3	25.0	29.0	21
	af8	24.6	25.0	2.9	0.6	11.6	20.0	31.0	25
	af9	26.5	26.0	2.1	0.5	8.0	23.0	31.0	20
	alb	24.8	25.5	3.0	1.0	12.2	20.0	29.0	10
	alg	20.2	20.0	1.0	0.2	4.8	19.0	22.0	19
	go1	33.0	–	–	–	–	–	–	>50
	go2	30.5	30.0	2.4	0.7	7.8	27.0	34.0	10
	go3	27.0	–	–	–	–	–	–	?
	ku1	26.0	26.0	1.2	0.3	4.6	24.0	28.0	15
	ku3	25.0	–	1.8	–	7.3	22.0	28.0	10
	na1	25.7	26.0	2.0	0.5	7.8	21.0	30.0	18
	na2	29.4	29.5	3.4	0.8	11.6	19.0	33.0	18
	sin	26.5	–	1.1	–	4.4	25.0	28.0	10

Table 14 Continued

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Adoral membranelles, number	sp1	39.1	40.0	3.1	0.6	7.9	32.0	43.0	25
	st1	27.9	28.0	1.3	0.3	4.7	25.0	30.0	21
	st2	27.9	28.0	2.4	0.7	8.6	24.0	31.0	13
	st3	29.4	29.0	2.0	–	7.0	26.0	34.0	30
	st4	25.7	25.0	1.5	0.3	5.9	23.0	30.0	21
	st5	29.5	–	2.2	0.6	7.3	26.0	33.0	11
Paroral kinetids, number	af2	13.6	14.0	3.1	0.7	22.8	8.0	19.0	21
	af3	10.6	11.0	2.1	0.5	19.6	5.0	14.0	21
	af4	8.6	8.0	1.8	0.4	20.6	6.0	12.0	21
	af5	10.2	10.0	2.1	0.5	20.5	6.0	14	21
	af6	9.0	9.0	1.7	0.4	19.3	6.0	11.0	21
	af7	12.5	13.0	1.9	0.4	14.9	6.0	16.0	21
	af9[s]	13.2	14.0	2.0	0.4	15.1	10.0	16.0	20
	alg	4.4	4.0	0.8	0.2	17.4	3.0	6.0	19
	go3	14.0	–	–	–	–	–	–	?
	ku3	10.7	–	1.2	–	10.8	8.0	12.0	10
	na1	7.1	7.0	1.4	0.4	19.7	5.0	10.0	14
	na2	12.9	13.0	2.3	0.5	17.9	8.0	18.0	18
	sin	14.8	–	0.8	–	5.3	14.0	16.0	10
	sp1[s]	23.6	23.0	4.2	1.0	17.7	19.0	33.0	18
	st1	13.4	13.0	1.8	0.4	13.2	11.0	17.0	21
	st2	12.2	13.0	2.0	0.5	16.1	9.0	15.0	13
	st3[q]	13.0	–	–	–	–	–	–	1
	st4	14.4	14.0	2.1	0.5	14.5	10.0	20.0	21
Frontal cirri, number	af2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af3	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af4	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af5	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af6	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af7	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af8	3.0	3.0	0.0	0.0	0.0	3.0	3.0	25
	af9	3.0	3.0	0.0	0.0	0.0	3.0	3.0	20
	alb	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	alg	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	go1	3.0	–	–	–	–	3.0	3.0	>50
	go2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	go3	3.0	–	–	–	–	–	–	
	ku1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	ku3	3.0	–	0.0	–	0.0	3.0	3.0	10
	na1	2.9	3.0	–	–	–	2.0	3.0	18
	na2	3.0	3.0	–	–	–	2.0	3.0	21
	sin	3.0	–	0.0	–	0.0	3.0	3.0	10
	sp1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	25
	st1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	st2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
	st3	3.0	3.0	0.0	–	0.0	3.0	3.0	30
	st4	3.0	3.0	0.0	–	0.0	3.0	3.0	21
	st5	3.0	–	0.0	0.0	0.0	3.0	3.0	17
Buccal cirri, number	af2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	af3	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21

Table 14 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Buccal cirri, number	af4	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	af5	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	af6	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	af7	1.0	1.0	–	–	–	0.0	1.0	21
	af8	1.0	1.0	0.0	0.0	0.0	1.0	1.0	25
	af9	1.0	1.0	0.0	0.0	0.0	1.0	1.0	20
	alb [b]	1.4	1.0	0.5	0.2	37.6	1.0	2.0	10
	alg	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	go2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	7
	go3	1.0	–	–	–	–	–	–	
	ku1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	ku3	1.0	–	0.0	–	0.0	1.0	1.0	10
	na1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	18
	na2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	18
	sin	1.0	–	0.0	–	0.0	1.0	1.0	10
	sp1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	25
	st1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	st2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
	st3	1.0	1.0	0.0	–	0.0	1.0	1.0	30
	st4	1.0	1.0	–	–	–	1.0	2.0	21
	st5	1.0	–	0.0	0.0	0.0	.1.0	1.0	17
Cirri in frontoventral row III, number [d]	st2	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
	st3	2.1	2.0	0.3	–	16.2	2.0	3.0	30
	st5	2.1	–	0.2	0.1	11.8	2.0	3.0	17
Cirri in frontoventral row IV, number [d]	st2	3.5	3.0	0.7	0.2	18.7	3.0	5.0	13
	st3	2.1	2.0	0.4	–	15.5	2.0	4.0	30
	st5	3.3	–	0.5	0.1	14.3	3.0	4.0	17
Cirri in frontoventral row V, number [d]	st2	6.9	7.0	1.3	0.4	19.1	5.0	9.0	13
	st3	6.9	7.0	0.8	–	11.6	6.0	8.0	30
	st4	4.7	5.0	0.6	0.1	12.4	4.0	6.0	21
	st5	7.2	–	0.5	0.1	7.4	6.0	8.0	17
Frontoventral cirri, number [j]	af1	11.0	11.0	0.9	0.2	12.0	10.0	13.0	12
	af2	5.5	5.0	0.9	0.2	15.8	5.0	7.0	21
	af3	5.9	6.0	0.8	0.2	13.0	4.0	7.0	21
	af4	3.8	3.0	1.1	0.2	28.3	3.0	6.0	21
	af5	4.8	5.0	0.8	0.2	17.4	3.0	6.0	21
	af6	5.0	5.0	0.4	0.1	7.8	4.0	6.0	21
	af7	3.1	3.0	0.5	0.1	15.2	3.0	5.0	21
	af8	5.0	5.0	0.0	0.0	0.0	5.0	5.0	25
	af9	5.1	5.0	0.5	0.1	10.4	4.0	6.0	19
	alb	9.0	9.5	1.4	0.4	15.7	6.0	10.0	10
	alg	4.8	5.0	1.0	0.2	19.8	4.0	8.0	19
	go1 [o]	10.0	–	–	–	–	9.0	11.0	>50
	go2	6.4	7.0	1.1	0.4	17.6	4.0	7.0	7
	ku1	7.0	7.0	0.0	0.0	0.0	7.0	7.0	15
	ku2	9.0	9.0	0.0	0.0	–	9.0	9.0	21
	ku3	2.0	–	0.0	–	0.0	2.0	2.0	10
	na1	6.4	7.0	1.1	0.3	17.0	5.0	9.0	18
	na2	11.5	11.0	2.0	0.5	17.4	8.0	16.0	17
	sin	2.0	–	0.0	–	0.0	2.0	2.0	10

Table 14 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Frontoventral cirri, number [j]	sp1	8.9	9.0	0.3	0.1	3.8	8.0	9.0	24
	st1	11.7	11.0	1.3	0.3	10.8	10.0	15.0	21
	st4	7.8	8.0	0.8	0.2	10.7	6.0	10.0	21
Frontoventral cirri, number of pairs	na1	2.7	3.0	0.6	0.1	22.3	2.0	4.0	18
	na2	4.1	4.0	0.9	0.2	22.2	2.0	6.0	17
Frontoterminal cirri, number	af2	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	af3	2.9	3.0	–	–	–	2.0	3.0	21
	af4	2.0	2.0	–	–	–	2.0	3.0	
	af5	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	af6	1.9	2.0	–	–	–	1.0	2.0	21
	af7	1.9	2.0	0.4	0.1	22.9	0.0	2.0	21
	af8	1.9	2.0	0.3	0.1	15.8	1.0	2.0	21
	alb	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	alg	2.4	2.0	–	–	–	2.0	3.0	19
	go1 [n]	17.0	–		–	–	17.0	18.0	>50
	go2	13.1	13.0	1.1	0.4	8.1	11.0	14.0	7
	go3 [n]	16.0	–	–	–	–	–	–	?
	ku2	2.0	2.0	0.0	0.0	–	2.0	2.0	21
	ku3	2.0	–	0.0	–	0.0	2.0	2.0	10
	na1	2.2	2.0	–	–	–	2.0	3.0	17
	na2	4.6	4.0	1.0	0.2	22.9	3.0	8.0	18
	sin	2.0	–	0.0	–	0.0	2.0	2.0	10
	st1	4.1	4.0	0.6	0.1	13.8	3.0	6.0	21
	st2	4.3	4.0	0.8	0.2	17.4	3.0	6.0	13
	st3	4.9	5.0	0.6	–	13.4	4.0	6.0	30
	st4	3.9	4.0	–	–	–	3.0	4.0	21
	st5	4.4	–	0.6	0.2	14.0	4.0	6.0	17
Frontal-ventral-transverse cirri, total number	af2	16.1	17.0	1.2	0.3	7.7	14.0	18.0	21
	af3	13.7	14.0	1.1	0.2	8.0	11.0	15.0	21
	af4	12.3	13.0	1.2	0.3	10.0	10.0	15.0	21
	af5	14.7	15.90	0.8	0.2	5.7	13.0	16.0	21
	af6	14.8	15.0	0.7	0.2	4.7	14.0	17.0	21
	af7	12.9	13.0	0.9	0.2	7.1	10.0	15.0	21
	st1	23.8	23.0	1.2	0.3	5.2	22.0	26.0	21
	st2 [f]	20.8	21.0	2.1	0.6	10.1	19.0	25.0	13
	st4 [f]	15.7	16.0	1.0	0.2	6.1	14.0	18.0	21
Postoral ventral cirri, number	go3	3.0	–	–	–	–	–	–	?
	ku3	3.0	–	0.0	–	0.0	3.0	3.0	10
	sin	3.0	–	0.0	–	0.0	3.0	3.0	10
Pretransverse ventral cirri, number	alb	1.9	2.0	0.4	0.1	18.9	1.0	2.0	10
	na1	1.9	2.0	–	–	–	1.0	2.0	17
	sin	2.0	–	0.0	–	0.0	2.0	2.0	10
	sp1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	25
	st2 [g]	1.5	2.0	–	–	–	0.0	2.0	13
	st2 [h]	1.3	1.0	–	–	–	1.0	2.0	13
Transverse cirri, number	af2	4.7	4.0	1.1	0.2	22.8	3.0	6.0	21
	af3	1.0	1.0	–	–	–	0.0	1.0	21
	af4	2.6	4.0	1.7	0.4	68.0	0.0	4.0	21
	af5	4.0	4.0	–	–	–	3.0	4.0	21
	af6	4.0	4.0	0.7	0.1	16.9	3.0	6.0	21

Table 14 Continued

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Transverse cirri, number	af7	3.9	4.0	0.5	0.1	12.4	2.0	4.0	21
	af8	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	af9	4.0	4.0	0.4	0.1	10.0	3.0	5.0	20
	alb	1.9	2.0	0.4	0.1	18.9	1.0	2.0	10
	alg	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	go2	2.7	3.0	0.5	0.2	18.0	2.0	3.0	7
	go3[e]	3.0	–	–	–	–	–	–	?
	ku1[e]	4.0	4.0	0.0	0.0	0.0	4.0	4.0	15
	ku2[e]	4.0	4.0	0.0	0.0	–	4.0	4.0	21
	ku3[e]	4.0	0	0.0	–	0.0	4.0	4.0	10
	na1	4.7	5.0	–	–	–	4.0	5.0	17
	na2[e]	2.6	3.0	1.0	0.2	38.3	0.0	4.0	20
	sin	4.0	–	0.0	–	0.0	4.0	4.0	10
	sp1	5.0	5.0	0.2	0.0	4.2	4.0	5.0	23
	st1[e]	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
	st2	1.9	2.0	–	–	–	1.0	2.0	13
	st3[e]	4.2	4.0	0.5	–	13.6	4.0	6.0	30
	st4[e]	4.1	4.0	0.4	0.1	9.5	3.0	5.0	21
	st5[e]	5.8	–	0.8	0.2	13.1	4.0	7.0	17
Pretransverse ventral cirri and transverse cirri, number	st2	4.7	5.0	1.1	0.3	23.6	2.0	6.0	13
Right marginal cirri, number	af1	23.0	22.0	2.7	0.7	11.0	18.0	27.0	12
	af2	16.6	17.0	2.9	0.6	17.2	10.0	21.0	21
	af3	17.8	18.0	2.9	0.6	16.0	12.0	23.0	21
	af4	16.5	16.0	2.3	0.5	13.7	11.0	20.0	21
	af5	19.5	19.0	2.3	0.5	12.0	16.0	26.0	21
	af6	17.7	17.0	2.5	0.5	14.2	13.0	23.0	21
	af7	18.8	18.0	1.8	0.4	9.5	15.0	22.0	21
	af8	22.6	23.0	1.2	0.3	5.5	20.0	24.0	24
	af9	19.0	19.5	1.9	0.4	9.8	16.0	22.0	20
	alb	15.5	15.5	2.7	0.8	17.2	12.0	21.0	10
	alg	18.3	18.0	1.8	0.4	10.0	15.0	24.0	19
	go1	23.0	–	–	–	–	18.0	27.0	>50
	go2	19.4	19.0	0.9	0.3	4.7	18.0	21.0	8
	go3	22.0	–	–	–	–	–	–	?
	ku1	21.3	22.0	1.9	0.5	9.0	18.0	25.0	15
	ku3	20.9	–	1.0	–	4.8	19.0	22.0	10
	na1	27.1	27.0	2.9	0.7	10.6	22.0	33.0	17
	na2	32.6	32.0	5.2	1.2	15.9	26.0	44.0	19
	sin	16.6	–	0.9	–	5.6	15.0	18.0	10
	sp1	24.0	24.0	3.2	0.6	13.2	16.0	29.0	25
	st1	25.4	24.0	4.2	0.9	16.5	21.0	33.0	21
	st2	20.5	19.0	3.5	1.0	17.2	16.0	27.0	13
	st3	26.9	27.0	1.9	–	7.2	23.0	30.0	30
	st4	22.7	23.0	1.7	0.4	7.4	20.0	27.0	21
	st5	25.8	–	2.0	0.5	7.6	23.0	29.0	13
Left marginal cirri, number	af1	14.5	14.5	1.6	0.4	11.0	12.0	17.0	12
	af2	11.0	11.0	1.9	0.4	17.5	7.0	15.0	21
	af3	11.8	12.0	2.4	0.5	20.3	6.0	16.0	21
	af4	12.3	12.0	2.9	0.6	23.3	8.0	22.0	21

Table 14 Continued

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Left marginal cirri, number	af5	14.8	15.0	1.3	0.3	8.5	12.0	17.0	21
	af6	12.6	12.0	1.6	0.3	12.6	10.0	16.0	21
	af7	12.3	12.0	1.1	0.2	8.6	11.0	15.0	21
	af8	18.8	19.0	1.7	0.3	8.9	15.0	22.0	24
	af9	13.6	13.5	1.6	0.4	11.8	11.0	17.0	20
	alb	18.1	19.0	3.6	1.1	19.7	13.0	22.0	10
	alg	12.9	13.0	1.8	0.4	13.5	10.0	16.0	19
	go1	14.0	–	–	–	–	12.0	15.0	>50
	go2	15.0	15.0	0.8	0.3	5.0	14.0	16.0	8
	go3	14.0	–	–	–	–	–	–	?
	ku1	16.3	16.0	1.0	0.3	6.3	15.0	18.0	15
	ku3	15.1	–	1.1	–	7.3	13.0	16.0	10
	na1	17.5	17.0	2.0	0.5	11.3	13.0	21.0	17
	na2	21.6	21.0	3.1	0.7	14.3	17.0	29.0	19
	sin	11.5	–	1.3	–	10.8	10.0	14.0	10
	sp1	14.9	14.0	2.0	0.4	13.4	12.0	20.0	25
	st1	17.3	18.0	2.6	0.6	15.1	13.0	21.0	21
	st2	14.9	15.0	1.6	0.4	10.4	13.0	18.0	13
	st3	17.4	17.0	2.0	–	11.6	16.0	22.0	30
	st4	15.7	16.0	1.3	0.3	8.3	13.0	19.0	21
	st5	17.7	–	5.2	1.4	29.6	17.0	21.0	13
Dorsal kineties, number	af2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af3	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af4	3.0	3.0	–	–	–	2.0	3.0	21
	af5	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af6	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af7	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af8	3.0	3.0	0.0	0.0	0.0	3.0	3.0	20
	af9	3.0	3.0	0.0	0.0	0.0	3.0	3.0	20
	alb	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	alg	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	go1	3.0	–	–	–	–	3.0	3.0	>50
	go2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
	go3	3.0	–	–	–	–	–	–	?
	ku1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	ku3	3.0	–	0.0	–	0.0	3.0	3.0	10
	na1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	na2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
	sin	3.0	–	0.0	–	0.0	3.0	3.0	10
	sp1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	24
	st1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	st2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
	st3	3.0	3.0	0.0	–	0.0	3.0	3.0	30
	st4	3.0	3.0	0.0	–	0.0	3.0	3.0	21
	st5	3.0	–	0.0	0.0	0.0	3.0	3.0	17
Dorsal kinety 1, number of bristles	af1	20.0	21.0	2.3	0.6	11.0	16.0	24.0	12
	go3	31.0	–	–	–	–	–	–	?
	ku3	15.6	–	1.1	–	6.9	14.0	18.0	10
	sin	18.0	–	1.6	–	8.7	16.0	22.0	10
	st2	19.4	19.0	3.0	0.8	15.7	15.0	26.0	13

Table 14 Continued

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Dorsal kinety 2, number of bristles	alb	15.5	16.5	2.2	0.7	14.2	12.0	18.0	10
	alg	9.1	9.0	1.2	0.3	13.1	7.0	11.0	19
	go3	21.0	–	–	–	–	–	–	?
	ku3	14.4	–	1.0	–	6.7	13.0	16.0	10
	na1	15.6	16.0	0.9	0.3	5.9	14.0	17.0	8
	na2	24.6	25.0	1.5	0.5	6.1	23.0	27.0	10
	sin	15.5	–	0.5	–	3.4	15.0	16.0	10
	st2	17.2	17.0	2.7	0.8	15.7	12.0	22.0	12
Dorsal kinety 3, number of bristles	go3	22.0	–	–	–	–	–	–	?
	ku3	18.6	–	0.8	–	4.5	17.0	20.0	10
	sin	21.8	–	1.9	–	8.9	19.0	25.0	10
	st2	20.8	21.0	3.1	0.9	14.8	15.0	26.0	13
Caudal cirri, number	af2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af3	3.0	3.0	–	–	–	2.0	3.0	21
	af4	2.8	3.0	0.7	0.2	25.4	0.0	3.0	21
	af5	2.5	3.0	0.7	0.2	29.7	1.0	3.0	21
	af6	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af7	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	af8	2.3	2.0	0.4	0.1	19.9	2.0	3.0	16
	af9	3.3	3.0	0.7	0.2	20.8	2.0	5.0	17
	alg	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	go1	3.0	–	–	–	–	3.0	3.0	>50
	go2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	5
	go3	3.0	–	–	–	–	–	–	?
	ku1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	ku3	3.0	–	0.0	–	0.0	3.0	3.0	10
	sin	3.0	–	0.0	–	0.0	3.0	3.0	10
	sp1	2.9	3.0	0.3	0.1	9.5	2.0	3.0	25
	st1	3.0	3.0	0.3	0.1	10.5	2.0	4.0	21
	st2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
	st3	3.0	3.0	0.0	–	0.0	3.0	3.0	30
	st4	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	st5	3.0	–	0.0	0.0	0.0	3.0	3.0	117

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known; if two values are known then they are listed as Min and Max; if only one value is known then it is listed as Mean), SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] According to Vd'ačný & Tirjaková (2006a, p. 93) five of 10 stained specimens have two buccal cirri; consequently five specimens have only one buccal cirrus because the minimum value is 1 and the maximum value is 2. This results in an arithmetic mean and median of 1.5; by contrast, in the original description an arithmetic mean of 1.4 and a medium of 1.0 are given.

[c] In the original description 4.0 is erroneously mentioned.

[d] See Fig. 23d for explanation. In row III, the frontal cirrus is not included.

[e] Pretransverse ventral cirri included. Populations *ku1* and *ku2* have invariable two pretransverse ventral cirri and two transverse cirri.

[f] Pretransverse ventral cirri and transverse cirri not included.

Table 14 Continued

[g] Pretransverse ventral cirri ahead of left transverse cirrus.

[h] Pretransverse ventral cirri ahead of right transverse cirrus.

[i] Macronuclear nodule measured (e.g., anteriormost) not specified. In *ku3* the diameter is given; in addition, in the text the minimum value is 2.8 (vs. 3.4 in table).

[j] In population *af1* the frontal cirri (I/1, II/3, III/3), the buccal cirrus (II/2), the frontoventral cirri (III/2, IV/3, VI/3, VI/4), and the postoral ventral cirri (IV/2, V/3, V/4) are included. In *af2–8*, *alg*, *na1*, *na2*, *st1*, and *st4* the frontal cirri, the buccal cirrus, and the frontoterminal cirri are not included. In population *ku1* the number of frontoventral cirri and postoral ventral cirri is given. In *ku2* the number of frontal cirri, frontoventral cirri III/2 and IV/3, and postoral ventral cirri is given (the frontoterminal cirri are not included). In *ku3* and *sin* the number of frontoventral cirri (III/2, IV/3) without frontoterminal cirri is given. In population *af9* the frontal cirri and the buccal cirrus are not included.

[k] Micronucleus measured (anteriormost) not specified. For *go2* the length is given.

[l] Value in %. For population *ku3* the ratio of body length:length of adoral zone is 2.1 on average. For population *sin* the ratio of body length:length of adoral zone is 2.0 (= 50% relative length) on average.

[m] The mean of 12 in Table 2 of Kamra et al. (2008) is obviously a printers error.

[n] The number of cirri forming the frontoventral row, originating from anlage VI, is given. Whether or not the two rearmost, slightly enlarged cirri (transverse cirrus and pretransverse ventral cirrus) are included is not clearly indicated.

[o] Comprises frontal cirri, buccal cirrus, and frontoventral cirri formed by anlagen III, IV, and V (the frontoventral cirri often form three pairs).

[p] From life. The sample size (n = 1) of the feature "Length of AZM" is obviously a printers error (correct n likely 19, as in other features).

[q] From Fig. 23e.

[r] Of 30 specimens investigated, one had three micronuclei.

[s] Note that Shin (1994) obviously confused endoral and paroral (see also text).

synonym of *G. affine* according to Berger (1999), has its type locality also in this area (see p. 168).

The type locality of *Trachelostyla canadensis* is a Prairie soil (chernozemic brown soils) from near the village of Matador (50°48'07"N 107°56'55"W), Southern Saskatchewan, Canada (Buitkamp & Wilbert 1974). Feeds on bacteria. Only one further record published, namely from Antarctic soil (Sudzuki 1979, p. 124).

The type locality of *G. singhii* is the Valley of Flowers National Park (30°41' to 30°48'N 179°33' to 79°46'E), India, where Kamra et al. (2008) found it in soil samples (0–10 cm). For a more detailed description of the Valley of Flowers, where permafrost is present for eight month, see Kamra et al. (2008); unfortunately, the authors did not provide exact data about the location of the sample site in this 88 km^2 large area. Food not described.

For most pre-1999 records of *G. affine*, see Berger (1999, p. 375). Foissner et al. (2001) characterised six soil populations of *G. affine* from almost all over the world, namely, (i) a beech forest in the surroundings of the city of Salzburg, Austria; (ii) a

very sandy pasture soil near the village of Alqasab, about 130 km north of Riyadh, Saudi Arabia; (iii) organic debris and sandy soil from the Sossus Vlei of the Namib desert, Namibia; (iv) very sandy soil around a *Welwitschia* plant near Swakopmund, Namibia; (v) cloud rain forest in the Henry Pitter National Park, Venezuela[1]; and (vi) gallery forest at the bank of the Rio Negro (Amazon floodplain), Manaus, Brazil. No relevant morphological differences could be found (see above). Further records of *G. affine* substantiated by morphological data: compost heap and rain-water channel underneath a roof, village of Schroetten, Deutsch Goritz, Austria (Eigner 1999, Fig. 11a–m); soil from Rwanda (Dragesco 2003, Fig. 10i–m); mosses from top of Cheonwang Mountain in Tongyeong (128°15'10"E 34°37'57"N), Korea (Kim & Shin 2006, misidentified as *G. algicola*, Fig. 14g–k); cultivated field soils in Misan-myon (38°02'N 127°01'E), Yonchon-gun, Kyonggi-do, Korea (Shin 1994, p. 119); Valley of Flowers National Park, India (Kamra et al. 2008; further details, see site description of synonym *G. singhii*).

Pre-1999 records overlooked by Berger (1999) and recent faunistic records are reviewed in the following paragraphs. Terrestrial habitats: common in natural forest stands in eastern Austria (Foissner et al. 2005, p. 627); common in primary dunes of the Dutch North Sea island Terschelling (Verhoeven 1999, p. 64); litter from a beech forest near the city of Göttingen, Germany (Bonkowski 1996, p. 35); soil (324 ppm Cl^-; pH 4.5; C/N 13.1) under a dune shrub in the North Sea island Norderney, Germany (Verhoeven 2001, p. 27; 2002, p. 189); common in various soils from Germany (Foissner 2000a, p. 257); abundant and common in solonetz soils in the Hortobágy National Park, Hungary (Szabó 1999, p. 249); highly productive chernozem soil near the village Hajdúszoboszló, Hungary (Szabó 2000, p. 14; 2001); coniferous and beech forest soils in the Bükk Hills, Hungary (Szabó 2003); rice field soil from the ISC (Istituto Sperimentale per la Cerealicoltura) near Verceli, Northern Italy (Schwarz 2003, p. 34; Schwarz & Frenzel 2003, p. 247); northern Italy and Sicilia (Dini et al. 1995, p. 69); moss on a sand dune in eastern part of the village of Eraclea Mare (corner Via Abeti and Via Pineta), Venetia, Italy (own observations); common in soils from an inland sand dune and a mixed deciduous forest in the Hoge Veluwe National Park in The Netherlands (Foissner & AL-Rasheid 2007, p. 204); soil from the riverside of the Danube river system in Slovakia (Tirjaková 1992, p. 77); with 46.6% frequency in soil under moss and common in dry mosses from Bratislava, Slovakia (Andelová & Tirjaková 2000, p. 35; Chrenková & Tirjaková 2000, p. 47); soil and litter in Malé Karpaty Mountains, Slovakia (Tirjaková & Vdacný 2004, p. 28); common in soil from an oak-hornbeam forest ecosystem in southwestern Slovakia (Tirjaková et al. 2002, p. 236; Holecová et al. 2005, p. 214); with 5% frequency in tree-holes from *Quercus dalechampii* and *Acer campestre* from various localities in Malé Karpaty Mountains, Slovakia (Tirjaková & Vdačný 2005, p. 26); very common (61–67% frequency) in all stages of decaying wood mass from 17 of 23 tree species from various sites in Slovakia (Bartošová & Tirjaková 2005, p.

[1] Note that this population is not identical with the *G. affine* studied by Foissner (2000), which is now assigned to *G. strenuum*.

39; 2008, p. 179); soil from the experimental site of the Sourhope Research Station near Kelso, Southern Scotland, UK (Finlay et al. 2001, p. 362; Esteban et al. 2006, p. 142); common in various soil samples from Saudi Arabia (Foissner et al. 2008a, p. 320); soil from a constructed mangrove wetland in the Futian Nature Reserve of Shenzhen, South China (Chen et al. 2009, p. 714); Japan (Hino & Momiki 1931, p. 45); common in soils of the Shimba Hills Nature Reserve (S5° E39°25'), Kenya (Foissner 1999, p. 323); very common (frequency 62%) in Namibian soils (Foissner et al. 2002a, p. 60); with 36% frequency in various soil samples from near the Tulane University campus, New Orleans, USA (Bamforth 2001, p. 200); microbiotic crusts composed of cyanobacteria, lichens, and bryophytes from desert soils of the Grand Canyon in northern Arizona, USA (Bamforth 2004, p. 413); bark of an *Acacia* tree from the Santa Rosa National Park in Costa Rica (Foissner 1994b, p. 295); common in rain forest soil from Brazil, Peru, and Costa Rica (Foissner 1997, p. 322); humic soil from near Cairns, Australia (Foissner 1997, p. 322); in 19 out of 26 soil samples from arid lands in Australia (Robinson et al. 2002, p. 452); in three of seven soil samples from the Mt. Field National Park in Tasmania (Foissner 1997, p. 322); in three of 20 soil samples from the Marion Island, southern oceans (Foissner 1996b, p. 284); arid soil (dominant plant *Ipomoea pescaprae*) from the Sisters peak, Ascension Island in the tropical South Atlantic (Wilkinson & Smith 2006, p. 410); common in soil from Antarctic islands (Signy Island, South Orkney Islands, Livingstone Island, South Shetland Islands; Foissner 1996a, p. 100).

Records of *G. affine* from limnetic habitats: Illach river, a clean mountain stream in Bavaria, Germany (Foissner 1997a, p. 183); with up to 5 ind. ml^{-1} in streamlets in the spring areas below the Velky Javorník near Bratislava, Slovakia (Tirjaková 1997, p. 15, 20; Tirjaková & Stloukal 2004, p. 16); in two of 15 sites from streams in the Poloniny National Park in the East Carpathian, Slovakia (Novikmec et al. 2007, p. 23); river Beli Lom, Bulgaria (Rusev et al. 1988, p. 40); Kiev and its environs, Ukraine (Dobrovlianski 1914, p. 46); Turkish inland waters (Çapar 2007a, p. 208); periphyton of Glubokoje Lake, Russia (Duplakoff 1933, p. 30); Donghu Lake, China (Shen & Gu 1965, p. 172); freshwater habitats in Lanzhou and Chongqing, China (Ning et al. 1993, p. 2; Su et al. 1988, p. 3; as *Gastrostyla affine*); planktonic with low frequency (3%) and <1% relative abundance in the shallow Lake Houhu near the city of Wuhan, China River (Song Biyu 2000, p. 148); Hanjiang River in China (Shen et al. 1994, p. 250; Jiang & Shen 2003, p. 787; Jiang 2006, p. 311); Beijing section of Juma River, China (Li et al. 2006, appendix, p. 6); freshwater habitats in polar regions (Petz et al. 2007, p. 401).

Gayewskaya (1924, p. 243) found *G. affine* in saltwater basins of the Kinburn Peninsula (Ukraine) and of the Crime at a salinity of 65‰ and a temperature of about 25 °C; however, this record is not substantiated by morphological data so that confusion with a halophile *Cladotricha* species cannot be excluded. Hino & Momiki (1931) found that *G. affine* is active from day 9 to 10 after adding rice straw decoction to the soil sample; certainly this cannot be generalised because now it is known that it occurs rather early (day 5 to 6) and is active for a long period.

Table 15 Origin of the frontal-ventral-transverse cirri primordia in *Gonostomum* species

Species (References)[a]	Primordium[b]					
	I	II	III	IV	V	VI
Proter						
Gonostomum affine (1)[f]	P (Fig. 120c–e in Berger 1999)	II/2 and OP (Fig. 120c, d in Berger 1999)	III/2? (Fig. 120d, e in Berger 1999)	IV/2? (Fig. 120d, e in Berger 1999)	V/4 (Fig. 120e in Berger 1999)	PP from OP and de novo (Fig. 120c–e in Berger 1999)
Gonostomum affine (2)	P (Fig. 11b, c)	II/2 (Fig. 11b, c)	III/2 (Fig. 11c)	IV/2, and IV/3? (Fig. 11c, e)	V/4 (Fig. 11c, e)	de novo PP (Fig. 11b)
Gonostomum algicola (3)	P (Fig. 18r, s, 19a)	II/2 (Fig. 18r, s, 19a, d)	III/2 (Fig. 18r, s, 19a)	IV/3 (Fig. 19e, f)	V/4 (Fig. 19e, f)	de novo PP (Fig. 19a, c, e)
Gonostomum kuehnelti (2)	P[d] (Fig. 16a, c)	II/2 (Fig. 16c, d)	III/2 (Fig. 16d)	IV/2, and IV/3? (Fig. 16d, e)	V/4 (Fig. 16d, e)	de novo PP and/or OP? (Fig. 16c, d)
Gonostomum strenuum (4)[c]	P (Fig. 122i in Berger 1999)	?	?	?	OP and rearmost cirri of row V (Fig. 122h in Berger 1999)	OP? (Fig. 122h, i in Berger 1999)
Gonostomum strenuum (5)[e]	P (Fig. 6 in Olmo & Téllez 1997)	II/2 (Fig. 6 in Olmo & Téllez 1997)	II/2 (Fig. 7 in Olmo & Téllez 1997)	cirri of IV (Fig. 8 in Olmo & Téllez 1997)	cirri of V (Fig. 8 in Olmo & Téllez 1997)	rearmost FT[g] (and/or de novo PP; Fig. 6 in Olmo & Téllez 1997)
Opisthe	I	II	III	IV	V	VI
Gonostomum affine (1)	? (P? OP?) (Fig. 120c–f in Berger 1999)	OP and II/2 (Fig. 120c–e in Berger 1999)	III/2 and OP? (Fig. 120c–e in Berger 1999)	IV/2? (Fig. 120d, e in Berger 1999)	V/3 (Fig. 120c–f in Berger 1999)	PP from OP and de novo (Fig. 120c–e in Berger 1999)
Gonostomum affine (2)	OP (Fig. 11b, c)	II/2 and/or OP? (Fig. 11c, e)	III/2 and/or OP? (Fig. 11c)	OP? de novo? (Fig. 11c, e)	V/3 (Fig. 11c)	de novo PP (Fig. 11b, c, e)
Gonostomum algicola (3)	OP (Fig. 19a, d)	OP (perhaps II/2 also involved; Fig. 19a, d, e)	OP? (Fig. 19c, d)	IV/2 (Fig. 19c, e, f)	V/3 (Fig. 19e, f)	de novo PP (Fig. 19a, c, e)
Gonostomum kuehnelti (2)	OP[d] (Fig. 16c)	II/2? (Fig. 16b)	OP (Fig. 16b)	OP? de novo? (Fig. 16c, d)	V/3 (Fig. 16d, e)	de novo PP or OP? (Fig. 16c, d)

Table 15 Continued

Species (References)[a]	Primordium[b]					
	I	II	III	IV	V	VI
Gonostomum strenuum (4)[c]	OP (Fig.	OP	OP?	OP?	OP and rearmost cirri of row V (Fig. 122h in Berger 1999)	de novo PP (Fig. 122h, i in Berger 1999)
Gonostomum strenuum (5)[e]	OP?	OP?	OP?	?	OP and rearmost cirri of row V? (Fig. 8 in Olmo & Téllez 1997)	rearmost FT[g] (and/or de novo PP; Fig. 6 in Olmo & Téllez 1997)

[a] 1 = Hemberger (1982); 2 = Eigner (1999); 3 = Foissner et al. (2002a); 4 = Song (1990); 5 = Olmo & Téllez (1997).

[b] Note that the anlagen II–V usually originate from two structures (e.g., anlage IV from parental cirri IV/3 ["proter"] and IV/2 ["opisthe"]) which fuse to form the primary primordia. Anlage I is formed more or less independently in proter and opisthe (that is, no primary primordium I is formed), and anlage VI usually originates de novo, that is, without participation of a parental structure. However, note that exceptions exist and some data are uncertain because the cirral pattern of *Gonostomum* species is not very stable and the cirri, from which many anlagen originate, are narrowly spaced in the frontal area! Abbreviations: OP = oral primordium, P = parental paroral, PP = primary primordium, FT = frontoterminal cirrus(i), I–VI = frontal-ventral-transverse cirri primordia (= streaks, = anlagen), II/2 = buccal cirrus (BC), III/2 = cirrus behind right frontal cirrus (parabuccal cirrus), ? = data uncertain (when in combination with another abbreviation) or origin not described and/or not recognisable from illustrations and/or micrographs.

[c] Note that Song (1990) confused endoral and paroral (see his Fig. 4). In addition, it is basically impossible to trace the exact origin of the primary primordia II–VI. For example, in the divider shown in Fig. 9 of Song (1990; = Fig. 122i in Berger 1999), seven streaks (including the short, rightmost one) are recognisable, although the buccal cirrus (II/2), which usually forms anlage II, is still intact.

[d] According to Eigner (1999, p. 37), anlagen I of proter and opisthe of *G. kuehnelti* are formed via a long primary primordium. However, this is not clearly supported by the illustrations provided. Probably, anlagen I of proter and opisthe are formed more or less independently as in other species (see also Foissner et al. 2002a, p. 809). Note that Eigner obviously did not use the term primary primordia in the usual sense, because he wrote that in *G. affine* anlage I is formed by "separate primary primordia" (Eigner 1999, p. 37).

[e] Olmo & Téllez (1997) provided no illustrations, but only micrographs of specimens impregnated with the pyridinated silver carbonate method. Thus, it is rather difficult (in several cases even impossible) to trace the origin of the anlagen.

[f] Note that cirrus IV/3 does not contribute to primordia formation according to Hemberger (1982; Fig. 120e–i in Berger 1999).

[g] According to Olmo & Téllez (1997, p. 193), anlage VI of *G. strenuum* originates from the rearmost frontoterminal cirrus. However, this is not clearly recognisable from their micrographs. The specimen illustrated in their Fig. 1 (= Fig. 23e in present book) has five frontoterminal cirri and according to the morphometric characterisation, the Spanish population has on average 4.9 cirri (median = 5; range 4–6; n = 30). Fig. 6 in their paper shows an early divider with a long primordium VI (leftmost arrow). Five parental frontoterminal cirri are still intact, and it is not clearly recognisable that anlage VI comes from the rearmost, sixth frontoterminal cirrus, which is rarely present. Perhaps only the anterior portion of the anlage comes from the rearmost frontoterminal cirrus and the rear portion originates, as is usual, for the other *Gonostomum* species, de novo. Detailed studies are needed to clear up the situation.

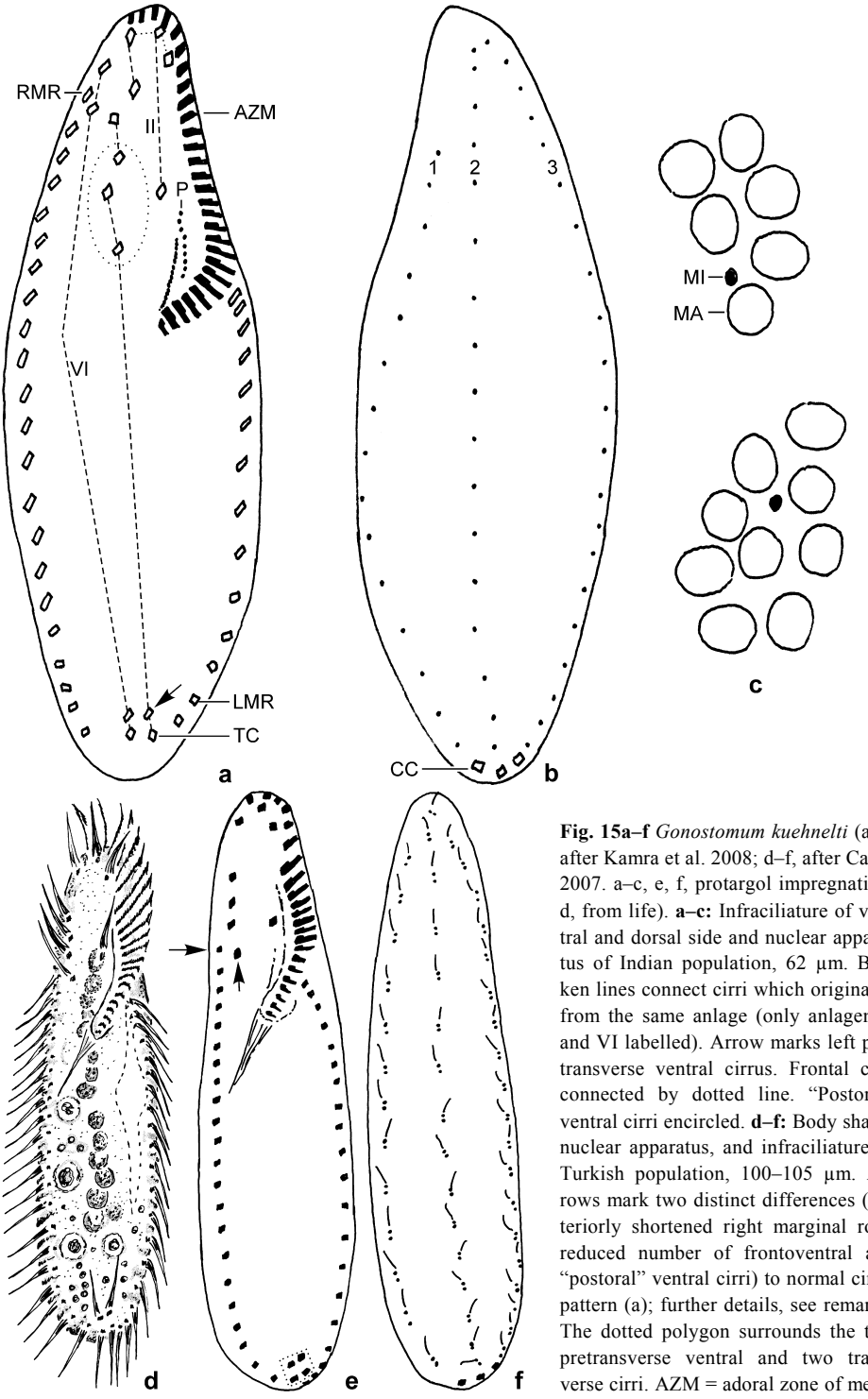


Fig. 15a–f *Gonostomum kuehnelti* (a–c, after Kamra et al. 2008; d–f, after Capar 2007. a–c, e, f, protargol impregnation; d, from life). **a–c:** Infraciliature of ventral and dorsal side and nuclear apparatus of Indian population, 62 µm. Broken lines connect cirri which originated from the same anlage (only anlagen II and VI labelled). Arrow marks left pretransverse ventral cirrus. Frontal cirri connected by dotted line. "Postoral" ventral cirri encircled. **d–f:** Body shape, nuclear apparatus, and infraciliature of Turkish population, 100–105 µm. Arrows mark two distinct differences (anteriorly shortened right marginal row; reduced number of frontoventral and "postoral" ventral cirri) to normal cirral pattern (a); further details, see remarks. The dotted polygon surrounds the two pretransverse ventral and two transverse cirri. AZM = adoral zone of mem-

***Gonostomum kuehnelti* Foissner, 1987**
(Fig. 15a–f, 16a–j, Tables 14, 15)

1987 ***Gonostomum kuehnelti* nov. spec.**[1] – Foissner, Sber. öst. Akad. Wiss., 195: 263, Abb. 37a–f, Tabelle 6 (Fig. 123a–f in Berger 1999; original description; the holotype slide [accession number 1986/48] and two paratype slides [1986/49, 50] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Aescht 2003, p. 389; 2008, p. 161).

1999 ***Gonostomum kuehnelti* Foissner, 1987** – Berger, Monographiae biol., 78: 391, Fig. 123a–f, Table 23 (detailed review).

1999 ***Gonostomum kuehnelti* Foissner, 1987** – Eigner, Europ. J. Protistol., 35: 35, Fig. 1–11, 33, Tables 1, 2 (Fig. 16a–j; morphology and morphogenesis of Austrian clone).

2001 ***Gonostomum kuehnelti* Foissner, 1987** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 29 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2007 ***Gonostomum kuehnelti* Foissner, 1987** – Çapar, Hacettepe J. Biol. & Chem., 35: 47, Fig. 4a–c (Fig. 15d–f; description of Turkish population; see remarks for some uncertainties).

2008 ***Gonostomum kuehnelti*** – Kamra, Kumar & Sapra, Indian J. Microbiol., 48: 382, Fig. 7, 14a–g, Table 5 (Fig. 15a–c; description of Indian population).

Nomenclature: Foissner (1987c) dedicated this species to Wilhelm Kühnelt, a founder of modern soil zoology. According to Foissner (1987c), one paratype slide has been deposited; however, according to Aescht (2003, 2008) two such slides are deposited in the Upper Austrian Museum in Linz.

Remarks: *Gonostomum kuehnelti* has, like the type species, the three postoral ventral cirri right of the posterior portion of the adoral zone. In addition, the transverse cirri II/1, III/1, and IV/1 are lacking whereas the transverse cirri V/1 and VI/1 and the two pretransverse ventral cirri (V/2 and VI/2)[2] of the plesiomorphic 18-cirri pattern are retained. The resulting reduced "18-cirri pattern" of *G. kuehnelti* is very stable according to the morphometric characterisation of the type population (Foissner 1987c). This is confirmed by the data on an Austrian and an Indian population which agree almost perfectly with the type population (Eigner 1999, Kamra et al. 2008). The sole appreciable difference is in the end of the left marginal row which is in the median of the cell in the type population, but at the level of the transverse cirri in the other populations (Fig. 123e in Berger 1999; Fig. 15a, 16a). The number of left marginal cirri is identical (Table 14). Eigner (1999) did not provide a detailed

← branelles, CC = caudal cirri, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = anterior end of right marginal row, TC = transverse cirri, II, VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 109.

[1] Foissner (1987c) provided the following diagnosis: In vivo etwa 60–90 × 25–35 µm großes *Gonostomum* mit durchschnittlich 15 kugelförmigen Makronucleus-Teilen und farblosen stäbchenförmigen subpellikulären Granula. Terricol.

[2] Foissner (1987c), Eigner (1999), Çapar (2007b), and Kamra et al. (2008) designate these cirri also as transverse cirri, which is, however, incorrect. Their position exactly ahead of the corresponding transverse cirri and the ontogenetic data (Eigner 1999; Fig. 16i) clearly show that they are homologous to the pretransverse ventral cirri of the oxytrichids (Fig. 6a in Berger 1999), urostyloids (Fig. 1a in Berger 2006a), and amphisiellids (Fig. 2a in Berger 2008).

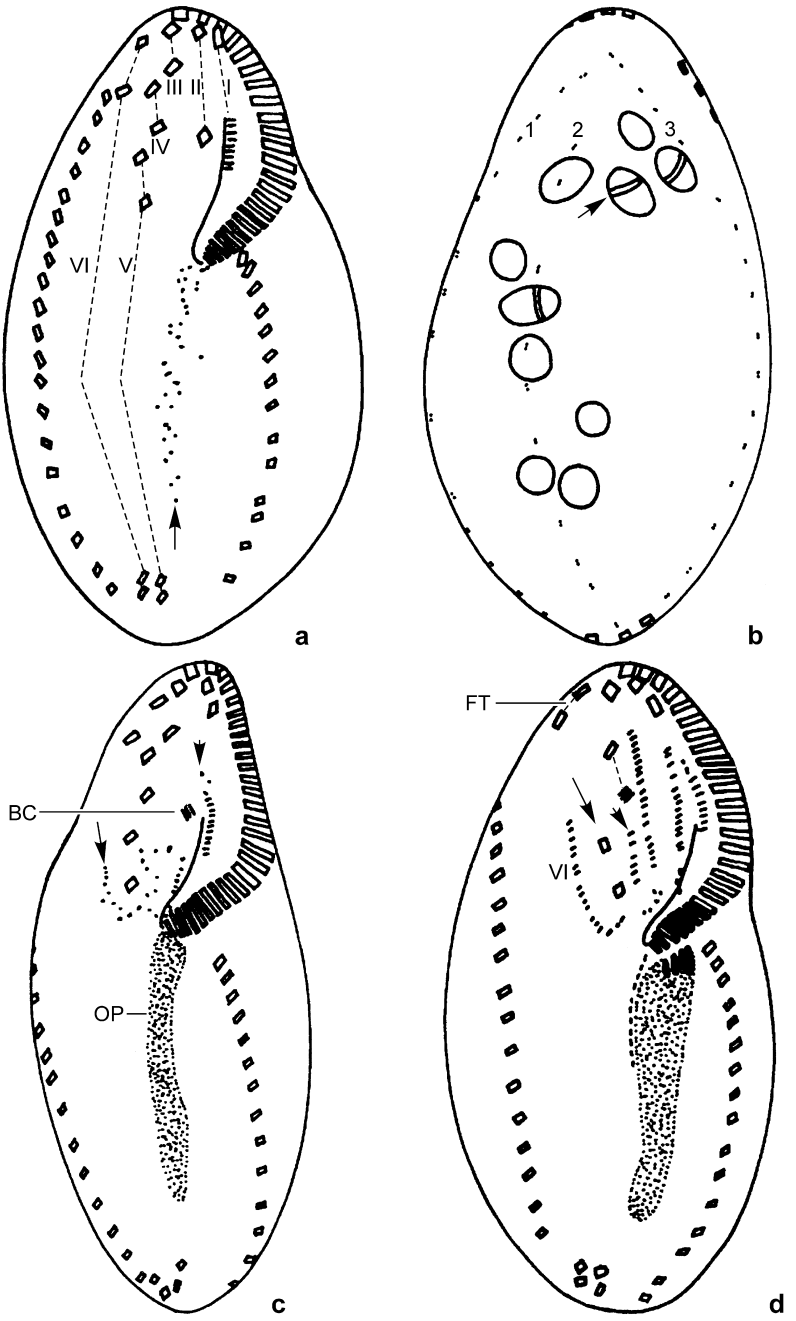


Fig. 16a–d *Gonostomum kuehnelti* (from Eigner 1999. Infraciliature of ventral [a, c, d] and dorsal side [b] and nuclear apparatus [b] after protargol impregnation). **a, b:** Very early divider, 56 µm. Arrow in (a) marks oral primordium, arrow in (b) denotes replication band. Broken lines connect cirri which originated from same anlage. **c:** Early divider, 63 µm. Short arrow marks anlage I of proter, long arrow denotes anlage VI. The buccal cirrus disaggregates to become anlage II. **d:** Middle divider, 50 µm. Short arrow marks

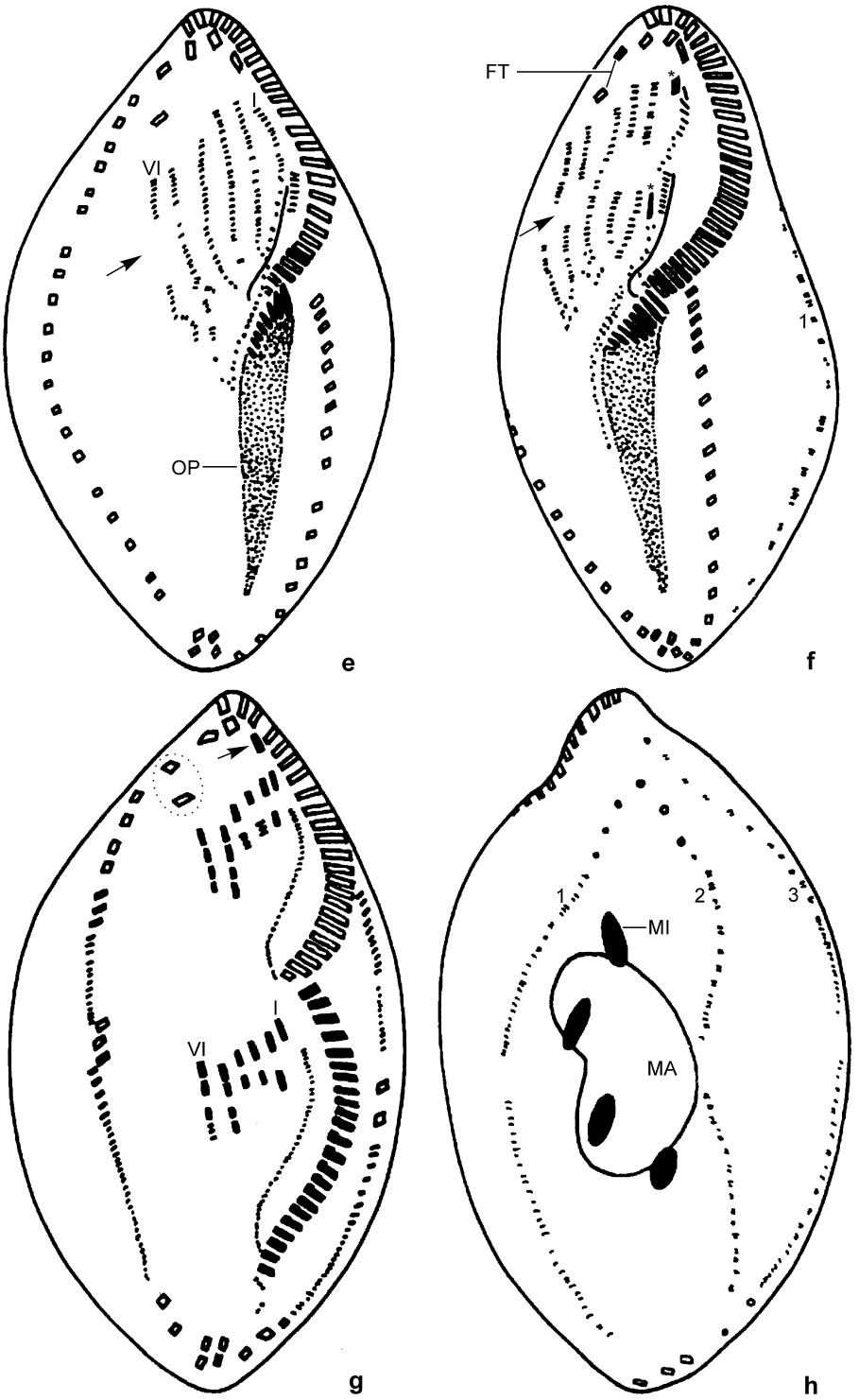
description of the interphasic morphology. Interestingly, he did not observe cortical granules, organelles reported from all other populations. Perhaps Eigner overlooked them because they are colourless and loosely arranged.

The cirral pattern of the population studied by Çapar (2007b) differs from the other populations in the arrangement of the frontoventral cirri and the lack of the postoral ventral cirri (Fig. 15d–f). Unfortunately, Çapar (2007b) did not discuss this difference. Whether this deviation indicates a new (sub)species or is due to inexact observations is not known and needs a reinvestigation of a population from the same locality.

Morphology: For a detailed morphological description of live specimens of the type population, see Berger (1999, p. 391). For summary of all morphometric data, see Table 14. In the first paragraph mainly the cirral pattern of the type population is described in greater detail than by Berger (1999). The Indian and Turkish populations are briefly characterised in the second and third paragraph.

Macronuclear nodules of type population often form two more or less distinct groups along median or slightly left of it (Fig. 123f in Berger 1999). Oral apparatus typically gonostomatid, adoral zone occupies 47% of body length on average (Table 14); paroral at anterior end of endoral, composed of about 10 loosely spaced basal bodies/cilia. Frontal-ventral-transverse cirri pattern of type very stable, invariable composed of 15 cirri (n = 15). Left frontal cirrus, as is usual for *Gonostomum*, displaced somewhat posteriad and slightly larger than the middle frontal cirrus. Buccal cirrus right of anterior end of paroral. Frontoventral cirri (cirrus III/2, IV/3, VI/3, VI/4) form roughly V-shaped pattern also known from many oxytrichids (Berger 1999); frontoterminal cirri (VI/3, VI/4) left of anterior part of right marginal row. "Postoral ventral" cirri form the characteristic, triangular pattern, that is, anterior cirrus (IV/2) slightly left of the middle (V/4) and rear (V/3) cirrus. Postoral area without cirri. Two pretransverse ventral cirri (V/2, VI/2) ahead of transverse cirri V/1 and VI/1; these four cirri form a quadrangular pattern (Fig. 123e in Berger 1999), an arrangement also known from other *Gonostomum*-species (e.g., Fig. 23a; Fig. 117d, 120a in Berger 1999). Right marginal row commences at level of frontal cirri in specimen illustrated, terminates roughly about at level of pretransverse ventral or transverse cirri. Left row begins left of rear end of adoral zone, terminates about in midline of cell, that is, J- shaped. All cirri about 20 µm long. Dorsal bristles in life about 3 µm long, arranged in the plesiomorphic pattern, that is, in three bipolar kineties; kinety 1 slightly shortened anteriorly, commences at 17% of body length in specimen illustrated (Fig. 123f in Berger 1999). Each kinety with a caudal cirrus.

← rear part of primary primordium IV, which originates de novo or from the oral primordium; the anterior portion is formed from the parental cirri IV/2 and IV/3 (connected by broken line). Long arrow denotes the two "postoral" ventral cirri V/3 (forms rear portion of primary primordium V) and V/4 (forms anterior portion of primary primordium V). BC = buccal cirrus, FT = frontoterminal cirri, OP = oral primordium, I–VI = frontal-ventral-transverse cirri "anlagen", 1–3 = dorsal kineties. Page 109.


I
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OP
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The Indian population studied by Kamra et al. (2008) agrees very well with the type material and therefore only additional, important, or deviating data are provided (Fig. 15a–c, Table 14): Cortical granules colourless, do not stain with protargol. Contractile vacuole just behind buccal vertex. Macronuclear nodules form two more or less distinct groups, a feature also present in type population (Fig. 15c; Fig. 123f in Berger 1999). According to Kamra et al. (2008), the cirri of *G. kuehnelti* are rather long: frontal cirri 14–16 µm; frontoventral cirri, frontoterminal cirri, and postoral cirri 10–12 µm; transverse cirri 17–19 µm; marginal cirri 11–13 µm; caudal cirri 14–15 µm.

As mentioned above, the Turkish population studied by Çapar (2007b) deviates distinctly from the other populations. Body size in life(?) 100–105 × 23–25 µm. Outline slender elliptical, margins slightly converging anteriorly; according to Çapar (2007b) also broad oval which is neither indicated by the measurements nor by the illustrations. Specimen illustrated with 15 macronuclear nodules arranged roughly in midline of cell, separated in two indistinct groups with eight (anterior) and seven (posterior) nodules. Contractile vacuole up to 10 µm across during diastole, with a distinct anterior and posterior collecting canal. Cortical granules 0.5–1.0 µm long and loosely arranged, no further details (e.g., colour, stainability with methyl-green pyronin) given. Cytoplasm colourless. Adoral zone gonostomatid, composed of 22 membranelles in specimen illustrated; according to text, occupying only 25% of body length which is, however, very likely a distinct underestimation; according to specimens illustrated, the relative length is about 38% (Fig. 15e); arrangement and fine structure of undulating membranes not described and not illustrated in detail. Frontal, ventral, and transverse cirri larger than remaining cirri. Three frontal cirri arranged roughly in *Gonostomum* pattern, that is, left cirrus distinctly displaced posteriad. Buccal cirrus right of anterior portion of paroral. Only four frontoventral and postoral ventral(?) cirri arranged in line right of middle portion of adoral zone (see remarks). Two pretransverse ventral cirri and two transverse cirri form quadrangular pattern. Right marginal row obviously distinctly shortened anteriorly, commences just at 25% of body length and composed of 22 cirri in specimen illustrated, ends near cell end (Fig. 15e). Left marginal row begins left of rear portion of adoral zone, terminates, like in type population, behind transverse cirri; composed of about 20 cirri in specimen illustrated. Three bipolar dorsal kineties, kinety 1 slightly short-

← **Fig. 16e–h** *Gonostomum kuehnelti* (from Eigner 1999. e–g, infraciliature of ventral side; h, infraciliature of dorsal side and nuclear apparatus; e–h, after protargol impregnation). **e:** Middle divider, 58 µm. Arrow marks zone where primary primordia divide. **f:** Late divider, 70 µm. Arrow marks division of primary primordia. As is usual, the frontoterminal cirri are not involved in primordia formation. Asterisks denote new left frontal cirrus both in proter and opisthe. **g:** Late divider, 50 µm. Parental frontoterminal cirri circled, arrow marks parental left frontal cirrus. Parental structures white, new black. **h:** The dorsal morphogenesis and the division of the nuclear apparatus proceed in the usual way (see also Fig. 16b, j). FT = frontoterminal cirri, OP = oral primordium, I, VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 109.

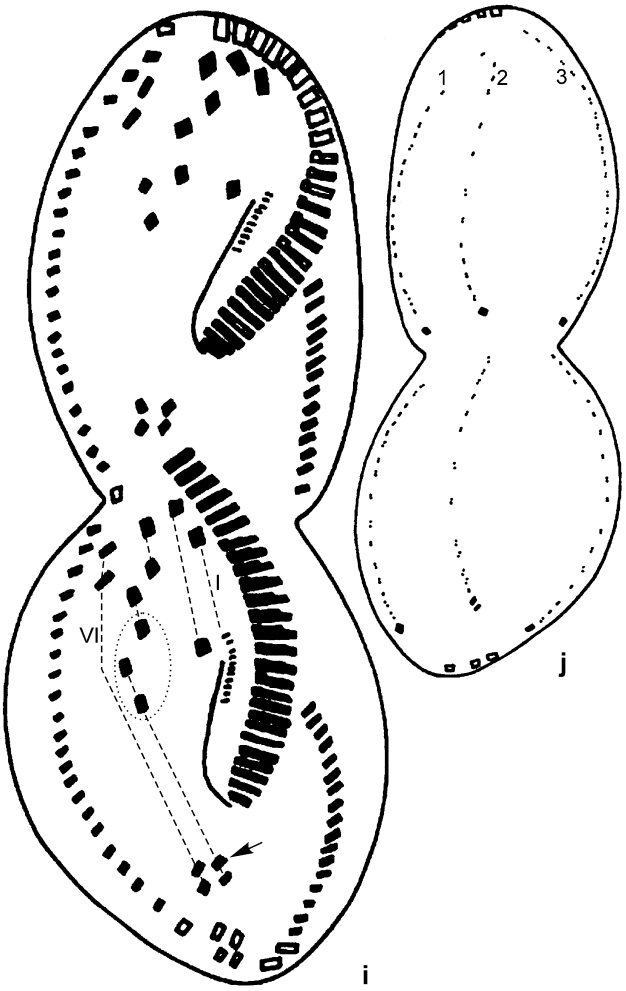


Fig. 16i, j *Gonostomum kuehnelti* (from Eigner 1999. Protargol impregnation). Infraciliature of ventral and dorsal side of a late divider, 62 µm. Broken lines connect cirri which originated from the same anlage (only shown for opisthe). Arrow marks pretransverse ventral cirri which have been incorrectly designated as transverse cirri in previous papers. Postoral ventral cirri (cirri IV/2, V/3, V/4) encircled. Parental cirri white, new black. The dorsal morphogenesis proceeds in the plesiomorphic manner (three bipolar kineties each forming one caudal cirrus). I, IV = frontal-ventral-transverse cirri anlagen, 1–3 = new dorsal kineties. Page 109.

ened anteriorly, kinety 2 composed of 16 bristles in specimen illustrated; each kinety with one caudal cirrus (Fig. 15f).

Cell division (Fig. 16a–j, Table 15): This part of the life cycle is described in detail by Eigner (1999) who also studied the morphogenesis of the type species. As expected, the process is identical in both species, except the formation of anlage I, which originates more or less independently in proter and opisthe in *G. affine*, but from a long primary primordium in *G. kuehnelti*, a feature not clearly recognisable from the published data (see below). Kamra et al. (2008) also studied cell division, but did not provide details, except the statement that the frontal-ventral-transverse cirri anlagen are formed via primary primordia, as is usual in *Gonostomum* (Berger & Foissner 1997, Berger 1999).

Cell division commences with the formation of an oral primordium roughly in the midline area between buccal vertex and pretransverse ventral cirri (Fig. 16a). Some macronuclear nodules show replication bands (Fig. 16b). Somewhat later, three anlagen originate from the oral primordium. In addition, the buccal cirrus begins to modify to anlage II. Anlage I originates from two basal bodies ahead of the parental paroral and from some basal bodies from the oral primordium which migrate over the endoral (Fig. 16c); these basal bodies proliferate and produce one long primary primordium for anlage I; whether this observation is indeed correct, should be checked by further studies. The buccal cirrus has modified to a streak and fuses with the leftmost anlage (except that forming anlage I) originating from the oral primordium to form the primary primordium II (Fig. 16c–e). Cirrus III/2 is modified to a streak and likely fuses with an anlage originating from the oral primordium to form primary primordium III. The cirri IV/2 and IV/3 also disorganise and fuse to an anlage and form, very likely together with a streak originating from the oral primordium, primary primordium IV. Cirri V/3 and V/4 are transformed to anlage V. Anlage VI originates de novo, as in *G. affine* (Eigner 1999, p. 37); however, a participation of the oral primordium cannot be excluded (Fig. 16c). As is usual, the frontoterminal cirri (VI/3, VI/4) do not participate in primordia formation (Fig. 16d–g). In middles stages each primary primordium divides so that six anlagen (I–VI) are present per filial product (Fig. 16e, f). In late and very late dividers the frontal-ventral-transverse cirri are formed in the usual way (Fig. 16g, i): anlage I forms the left frontal cirrus (I/1), and in the opisthe also the undulating membranes, at least to certain extent (the parental undulating membranes are retained for the proter, although some reorganisation could not be excluded with certainty by Eigner 1999); anlage II forms the buccal cirrus (II/2) and the middle frontal cirrus (II/3); anlage III forms the parabuccal cirrus (III/2) and the right frontal cirrus (III/3); anlage IV forms the anteriormost postoral ventral cirrus (IV/2) and the rearmost frontoventral cirrus (IV/3); anlage V forms the left transverse cirrus (V/1), the left pretransverse ventral cirrus (V/2) and the rearmost and middle postoral ventral cirrus (V/3, V/4); and anlage VI forms the right transverse cirrus (VI/1), the right pretransverse ventral cirrus (VI/2), and the two frontoterminal cirri (VI/3, VI/4).

The new marginal rows and dorsal kineties originate by intrakinetal proliferation at two levels in the parental structures. Usually one caudal cirrus is formed at the end of each kinety (Fig. 16g–j); only rarely two cirri per kinety are set up, but obviously invariably only one cirrus per kinety remains (Table 14). No parental cirri are retained in the filial products.

The macronuclear nodules fuse to a single mass, which later apportions into the proter and the opisthe where the species-specific number of nodules is attained during the late stages of morphogenesis (Fig. 16n).

Occurrence and ecology: *Gonostomum kuehnelti* is an edaphic species. The type locality is near the village of Seekirchen (Salzburg, Austria), where Foissner (1987a) discovered it in an organically farmed field; the soil sample (0–15 cm; 600 m altitude; pH 6.0) was collected on 24.03.1984 and the collection site is described in de-

tail by Foissner et al. (1987; site G). For some pre-1999 records, see Berger (1999, p. 392).

Records substantiated by morphological data: forest soil next to the village of Schroetten, Styria, Austria (Eigner 1999); moss on a sand dune in the eastern part of the village of Eraclea Mare (corner Via Abeti and Via Pineta), Venetia, Italy (own observations); soil samples from the Valley of Flowers, which lies between 30°41' to 30°48'N and 79°33' to 79°46'E in the Chamoli Garhwal Himalayas (3250–6750 m above sea-level), India (Kamra et al. 2008; see this paper for more details on this extraordinary sampling site). The deviating Turkish population is from soil samples (0–10 cm) collected from the flooded area[1] of the Gelingüllü Dam Lake (39°36'30"N 35°03'20"E), Yozgat Province, Central Anatolia region, Turkey (Çapar 2007a, p. 208; 2007b).

Further records: two natural forest stands (Johannser Kogel, *Eu-Fagenion*; Müllerboden, *Pruno-Fraxinetum*) in eastern Austria (Foissner et al. 2005, p. 627); Beech forest on the "Kleinen Gudenberg" near Zierenberg, a small town near Kassel, Germany (Bonkowski 1996, p. 35; Foissner 2000a, p. 257); soil and litter in Malé Karpaty Mountains, Slovakia (Tirjaková & Vdacný 2004, p. 28); soil samples from an oak-hornbeam forest ecosystem in south-western Slovakia (Holecová et al. 2005, p. 215; Bartošová et al. 2007, p. 3); with 2% frequency in tree-holes from *Quercus dalechampii* and *Acer campestre* from various localities in Malé Karpaty Mountains, Slovakia (Tirjaková & Vdacný 2005, p. 26); in three of nine soil samples collected in the Shimba Hills Nature Reserve (S5° E39°25'), Kenya (Foissner 1999, p. 323); with a frequency of 6% in Namibian soils (Foissner et al. 2002a, p. 60); in *Deschampsia antarctica* grass swards of Antarctic islands (Signy Island, South Orkney Islands, Livingstone Island, South Shetland Islands; Foissner 1996a, p. 100).

Eigner (1999) set up the raw cultures with local spring water. The clone was maintained at room temperature and baker's yeast was used as food.

Gonostomum algicola Gellért, 1942

(Fig. 17a, b, 18a–s, 19a–t, 20a–g, Tables 14, 15)

1942 ***Gonostomum algicola* n. sp.** – Gellért, Acta Sci. math.-nat. Univ. Kolozsvar., 8: 23, Fig. 23, 24 (Fig. 17a, b; original description in Hungarian, thus diagnosis not quoted verbatim; likely non of the opalblue-stained specimens of the type population is still available).

1974 ***Gonostomum algicolum* Gellért** – Stiller, Fauna hung., 115: 93, Fig. 54B (redrawing of Fig. 17a, b; guide to Hungarian hypotrichs).

1984 ***Gonostomum algicola* Gellért, 1942** – Maeda & Carey, Bull. Br. Mus. nat. Hist. (Zool.)., 47: 12, Fig. 5 (redrawing of Fig. 17a; detailed review of *Trachelostyla* and *Gonostomum*).

1999 ***Gonostomum affine* (Stein, 1859) Sterki, 1878** – Berger, Monographiae biol., 78: 369 (pro parte), only Fig. 118j, k (Fig. 17a, b; revision, see remarks).

2001 ***Gonostomum algicola* Gellért, 1942** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 29 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

[1] I suppose that the samples where collected when the "flooded" area was not underwater.

2002 ***Gonostomum algicola* Gellért, 1942** [1] – Foissner, Agatha & Berger, Denisia, 5: 799, Fig. 174a–w, 175a–t, 399a–g, Tables 154, 155 (Fig. 18a–s, 19a–t, 20a–g; detailed redescription, morphogenesis, and neotypification. Six slides [accession numbers 2002/134–139] are deposited in the Upper Austrian Museum in Linz; further details, see nomenclature).

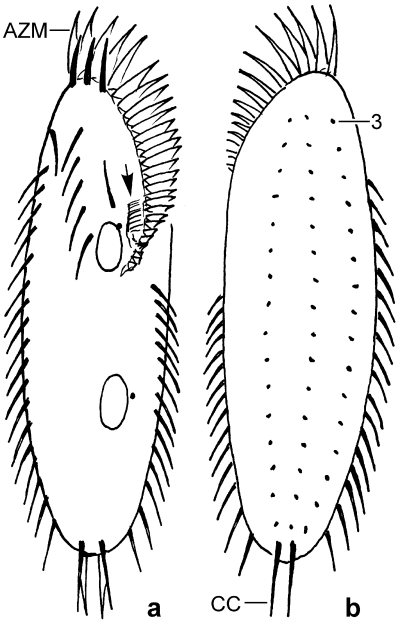


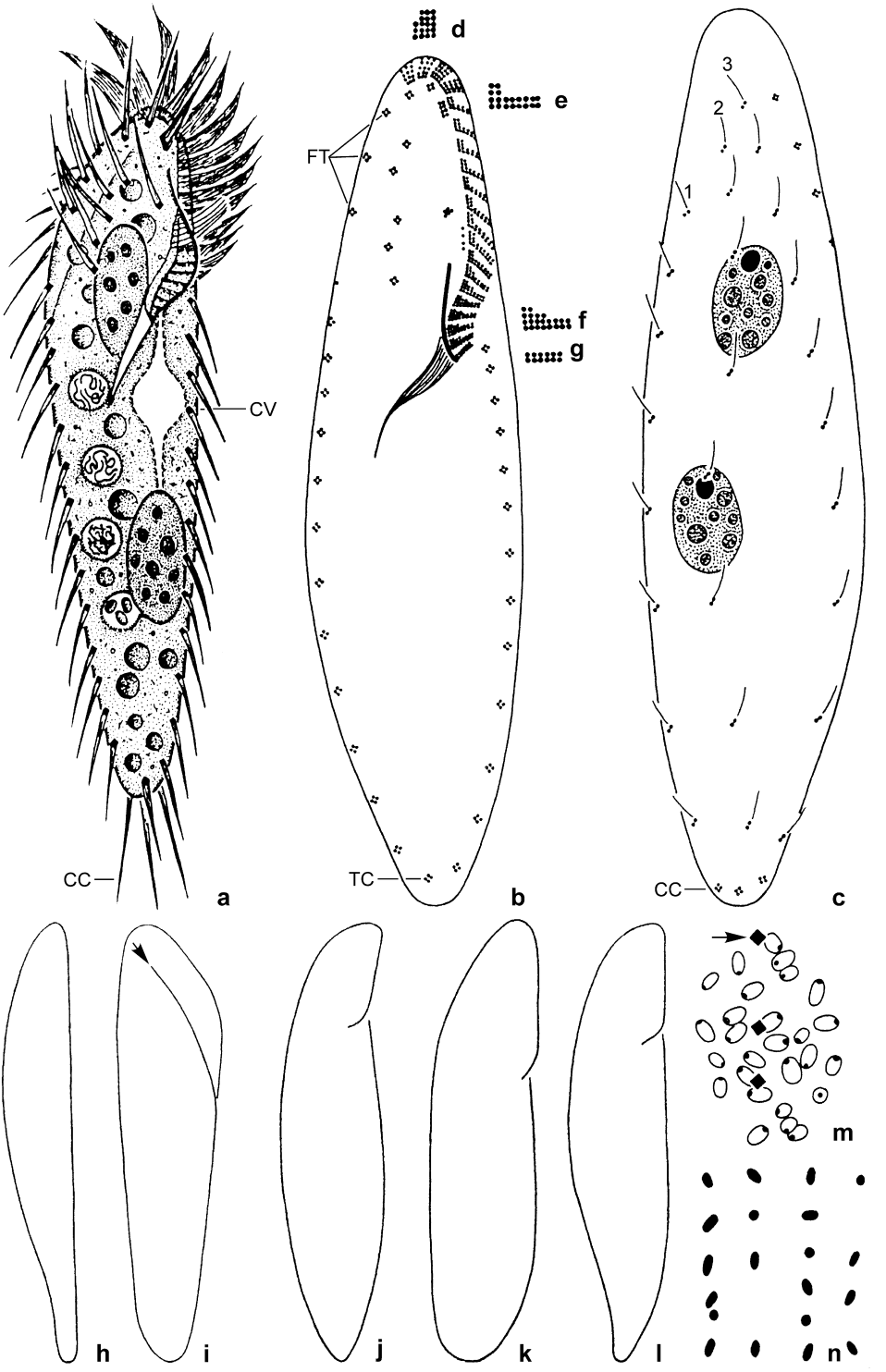
Fig. 17a, b *Gonostomum algicola* (after Gellért 1942. Sublimate fixation and opal-blue preparation after Bresslau). Infraciliature of ventral and dorsal side and nuclear apparatus, 60–100 µm. Arrow marks paroral which is composed of only few, widely spaced cilia. For explanation of discrepancy between Hungarian population and neotype material concerning transverse and caudal cirri, see text. Body length:width ratio 3:1. AZM = distal end of adoral zone of membranelles, CC = caudal cirri, 3 = dorsal kinety 3. Page 116.

Nomenclature: No derivation of the name is given in the original description, my review (Berger 1999), and the monograph by Foissner et al. (2002a). The species-group name *algicola* is a composite of the Latin noun *alga* (seaweed; obviously algae in present case), the thematic vowel *·i-*, and the Latin suffix *-cola* (from the noun *incola*; inhabitant, dweller) and obviously refers to the fact that Gellért (1942) discovered this species in the algae film covering the bark of trees. Usually, species-group names ending with *-cola* are considered as appositive substantives and are thus (usually) not changed when transferred to a genus of different gender (Werner 1972, p. 138). Thus, the adjustment of the species-group name from *algicola* to the neuter form *algicolum* proposed by Stiller (1974) is not accepted.

Foissner et al. (2002a, p. 39) deposited six slides in the Upper Austrian Museum in Linz and designated all of them as neotypes in their Table 1. According to Aescht (2008, p. 141), however, only the slide with the accession number 2002/134 is labelled as neotype, while the remaining five are lettered as vouchers. The slide containing the neotype specimen (Fig. 174b, c in Foissner et al. 2002a; Fig. 18b, c in present book) is the holoneotype slide, the others are the paraneotype slides.

Remarks: *Gonostomum algicola* was described by Gellért (1942) in Hungarian. Borror (1972) cited Gellért's paper in the reference section and listed "*Oxytricha tet-*

[1] Foissner et al. (2002a) provided the following improved diagnosis: Size about 80 × 22 µm in vivo; lanceolate. 2 macronuclear nodules. Cortical granules colourless and loosely spaced. Cirri conspicuously fine, most comprising only 4 cilia. On average 18 right marginal, 13 left marginal, 2 frontoterminal, 5 frontoventral, and 3 caudal cirri; 1 buccal cirrus slightly above paroral and 1 transverse cirrus near posterior end. Adoral zone of membranelles about one third of body length, composed of 20 membranelles on average. 3–6, usually 4 paroral kinetids.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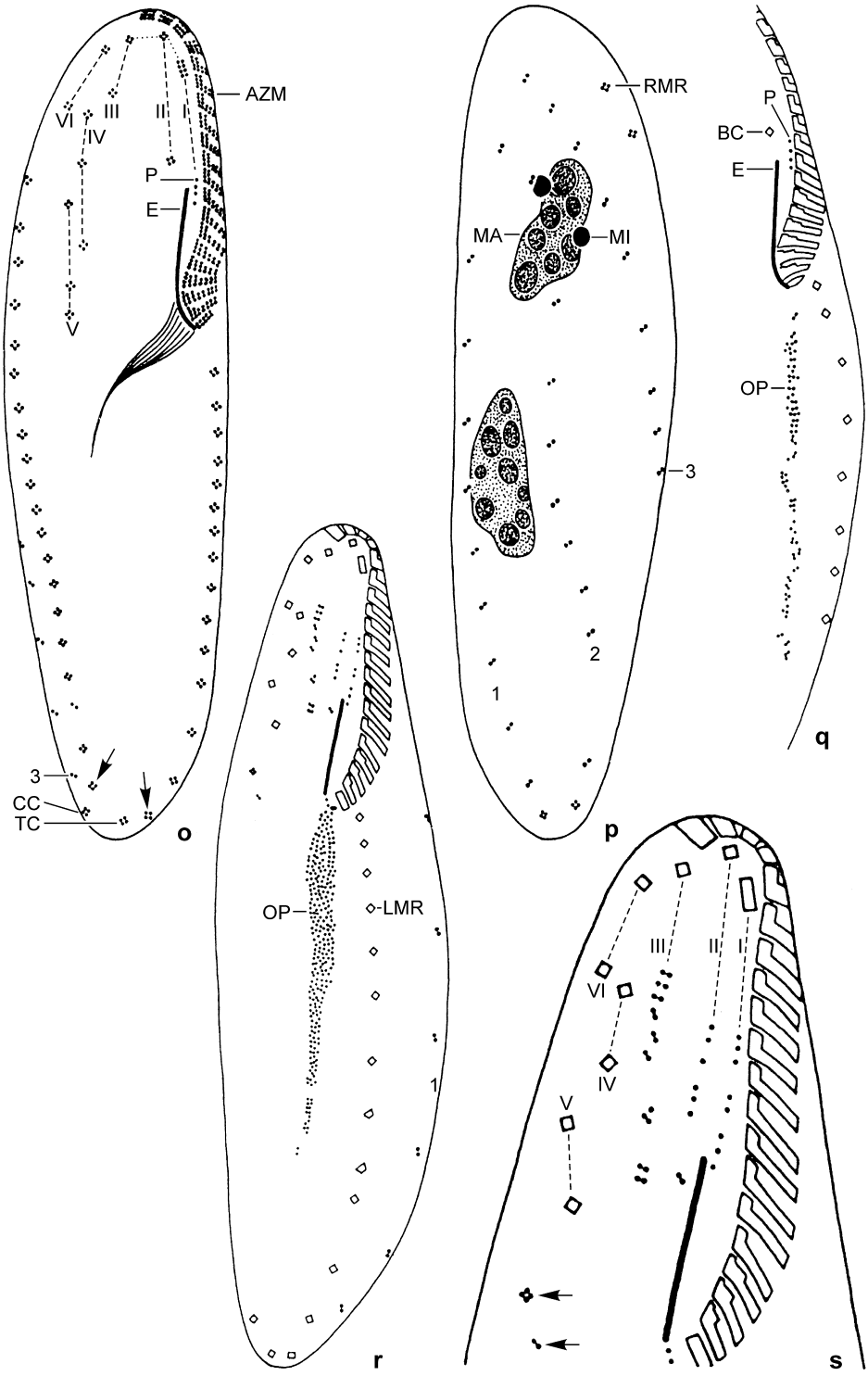
racirrata Gellért, 1942" (basionym: *Steinia tetracirrata* Gellért, 1942: for review, see Berger 1999, p. 317), another species described in this paper, but did not mention *G. algicola*, indicating that he overlooked this species. Stiller (1974) reviewed it in her paper about hypotrichous ciliates from Hungary. Buitkamp (1977, p. 125) radically submerged all *Gonostomum* species described so far in *G. affine* and simultaneously transferred it to *Trachelostyla*. Interestingly, he overlooked *G. algicola*, likely because it was not mentioned in the compilation by Borror (1972). Maeda & Carey (1984) accepted it as valid species and listed *Trachelostyla canadensis* and *Trachelostyla affine* sensu Buitkamp (1977) as synonyms. However, they justified the synonymy with some irrelevant features, for example, three frontal cirri, one buccal cirrus, two macronuclear nodules, lack of cirri in postoral area, two transverse cirri. They also discussed the main difference between *T. canadensis* and *T. affine* sensu Buitkamp (1977) and *Gonostomum algicola*, namely the unlike number of caudal cirri (three in both populations described by Buitkamp vs. two in *G. algicola*), but did not try to explain this discrepancy.

Foissner (1998, p. 203) was the first who (knowingly?)[1] synonymised *G. algicola* with *G. affine*; but simultaneously he (p. 211, footnote 9) questioned the synonymy. On the other hand, Foissner (1998, p. 210) put *Trachelostyla canadensis* into the synonymy of *G. algicola* (see *G. affine* for more details on *T. canadensis*). Although I cited Foissner (1998) in my review on the oxytrichids, I unnecessarily classified *G. algicola* again as new synonym of *G. affine*, likewise without providing an explicit foundation (Berger 1999). I presumed that this act needs no explanation because of the high similarity of the two species in habitus and cirral pattern having regard to the high variability of the cirral pattern described for *G. affine*. Obviously I simply overlooked that Foissner (1998) already had synonymised them, but I already made a note that W. Foissner considered it as valid species on the basis of new data (Berger 1999, p. 370). These new results were published by Foissner et al. (2002a) in their monograph on the soil ciliates from Namibia, and we used the African material to neotypify *G. algicola*, a mandatory act because the sophisticated details (e.g., exact cirral pattern in rear body portion) of *G. algicola* are not known from the

← **Fig. 18a–n** *Gonostomum algicola* (neotype population from Foissner et al. 2002a. a, h–l, n, from life [i–l, redrawn from video records]; b–g, m, protargol impregnation). **a:** Ventral view of representative specimen, 91 µm. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of neotype specimen, 83 µm. **d–g:** Structure of membranelles in frontal, middle, and proximal portion of adoral zone. **h:** Right lateral view. **i:** Dorsal view of a shape variant showing furrow along right marginal row. **j–l:** Ventral view of shape variants. **m:** Subcortical structures, possibly mitochondria; arrow marks cirrus. **n:** The cortical granules are highly refractive, but difficult to recognise because small (0.8 × 0.5 µm), colourless, and loosely spaced. CC = caudal cirri, CV = contractile vacuole, FT = frontoterminal cirri, TC = transverse cirrus, 1–3 = dorsal kineties. Page 116.

[1] I guess that Foissner (1998) supposed that *G. algicola* was already synonymised – like the other *Gonostomum* species described by Gellért – with *G. affine* by Buitkamp (1977); likely for that reason he did not provide a foundation for the synonymy. However, as explained above, Buitkamp (1977) has overlooked *G. algicola*.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original description. The Namibian specimens agreed with the original description of *G. algicola* in several important features, namely, (i) size (prepared specimens 52–95 and 60–100 µm, respectively), (ii) length of adoral zone (40% of body length vs. usually around 50% in congeners), (iii) pattern and number of frontoventral and frontoterminal cirri, and (iv) low number of paroral cilia (cp. Fig. 17a and Fig. 18b, o). Of course there are also some differences between the neotype and the Hungarian population, namely in the number of transverse cirri (1 vs. 4) and caudal cirri (3 vs. 2). However, both features are rather difficult to ascertain without ontogenetic data, even in protargol-preparations, because all cirri have a very similar size and are close together due to the narrow body end. Thus, it is reasonable to assume that Gellért, who studied only opal blue-treated, air-dried, morphostatic specimens, confound the posteriormost marginal cirri and the right caudal cirrus, which is often laterally inserted, as transverse cirri (Fig. 17a, b, 18o); consequently, we supposed that he counted four (ventral) transverse cirri and only two (dorsal) caudal cirri. However, one also cannot exclude that Gellért (1942) misinterpreted the three caudal cirri[1] as transverse cirri in Fig. 17a, b and therefore his population had four (1 + 3) "transverse" cirri. Some other small differences, for example, in the arrangement of the dorsal kineties and the length of the right marginal row, are likely also based on misobservations by Gellért due to the relatively imprecise staining method.

The Korean population studied by Kim & Shin (2006) differs from the neotype population in the number of transverse and pretransverse ventral cirri (two vs. one; Table 14) and by the distinctly higher number of paroral cilia, indicating that the identification is incorrect. The neotype population has 3–6, usually four paroral cilia (Fig. 17a, b), whereas the Korean specimen illustrated has 10 cilia (Fig. 14g–k). The average for *G. affine* is 9–14 (range 5–19; Table 14) strongly indicating that *G. algicola* sensu Kim & Shin (2006) is *G. affine*. Kim & Shin (2006) considered – obviously referring to Foissner (1998) – *Trachelostyla canadensis* as junior synonym of *Gonostomum algicola* (details see above and at *G. affine*). They compared their population in detail with the congeners. However, their separation from *G. affine* is incorrect because the Korean specimens have exactly the cirral pattern of the type

← **Fig. 18o–s** *Gonostomum algicola* (from Foissner et al. 2002a. Protargol impregnation). Broken lines connect cirri originating from same anlage. **o, p:** Infraciliature of ventral and dorsal side and nuclear apparatus, 65 µm. Arrows mark rearmost marginal cirri. **q:** Ventral view of a very early divider showing apokinetal formation of oral primordium. **r, s:** Ventral view (total and detail) of an early divider showing origin of proter anlagen I–III from parental structures, whereas anlage VI (arrows) originates de novo. AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri, E = endoral, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, OP = oral primordium, P = paroral, RMR = right marginal row, TC = transverse cirrus, I–VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 116.

[1] Gellért illustrated three dorsal kineties which corresponds the ground pattern of *Gonostomum* and the hypotrichs in general (Berger 2008). In addition, we have to assume that *G. algicola* has, like the congeners and the supposed last common ancestor of the hypotrichs (Fig. 2a, b), one caudal cirrus attached to the rear end of each dorsal kinety.

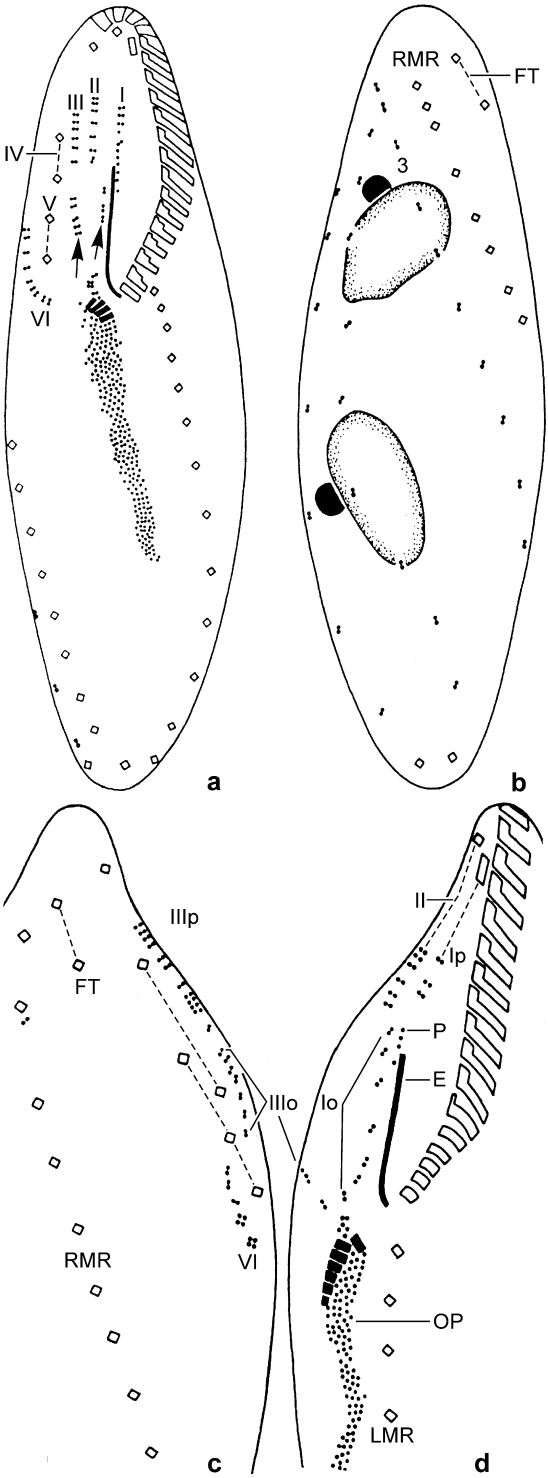


Fig. 19a–d *Gonostomum algicola* (from Foissner et al. 2002. Protargol impregnation). Origin of cirral anlagen and adoral membranelles, which commence to differentiate, as is usual, at the anterior end of the oral primordium. Basal bodies from the anterior end of the oral primordium migrate anteriad and organise to two streaks (arrows in a). The left streak becomes opisthe's anlage Io, the right (IIIo) touches anlage III of the proter (IIIp). In the specimen shown in (a), we could not exclude that the right anlage (left arrow) did not originate by migration of basal bodies from the oral primordium, but from a cirrus because about 15% of the specimens have a cirrus at this site. Note that anlage VI, which originates de novo, is distinctly separate from the oral primordium and the frontoterminal cirri. E = endoral, FT = frontoterminal cirri, LMR = left marginal row, OP = oral primordium, P = paroral, RMR = right marginal row, I–VI = frontal-ventral-transverse cirri anlagen (o marks anlagen for opisthe, p for proter; somewhat later they fuse to form the so-called primary primordia), 3 = dorsal kinety 3. Page 116.

species. Thus, I classify *Gonostomum algicola* sensu Kim & Shin (2006) as *G. affine* (Fig. 14g–k).

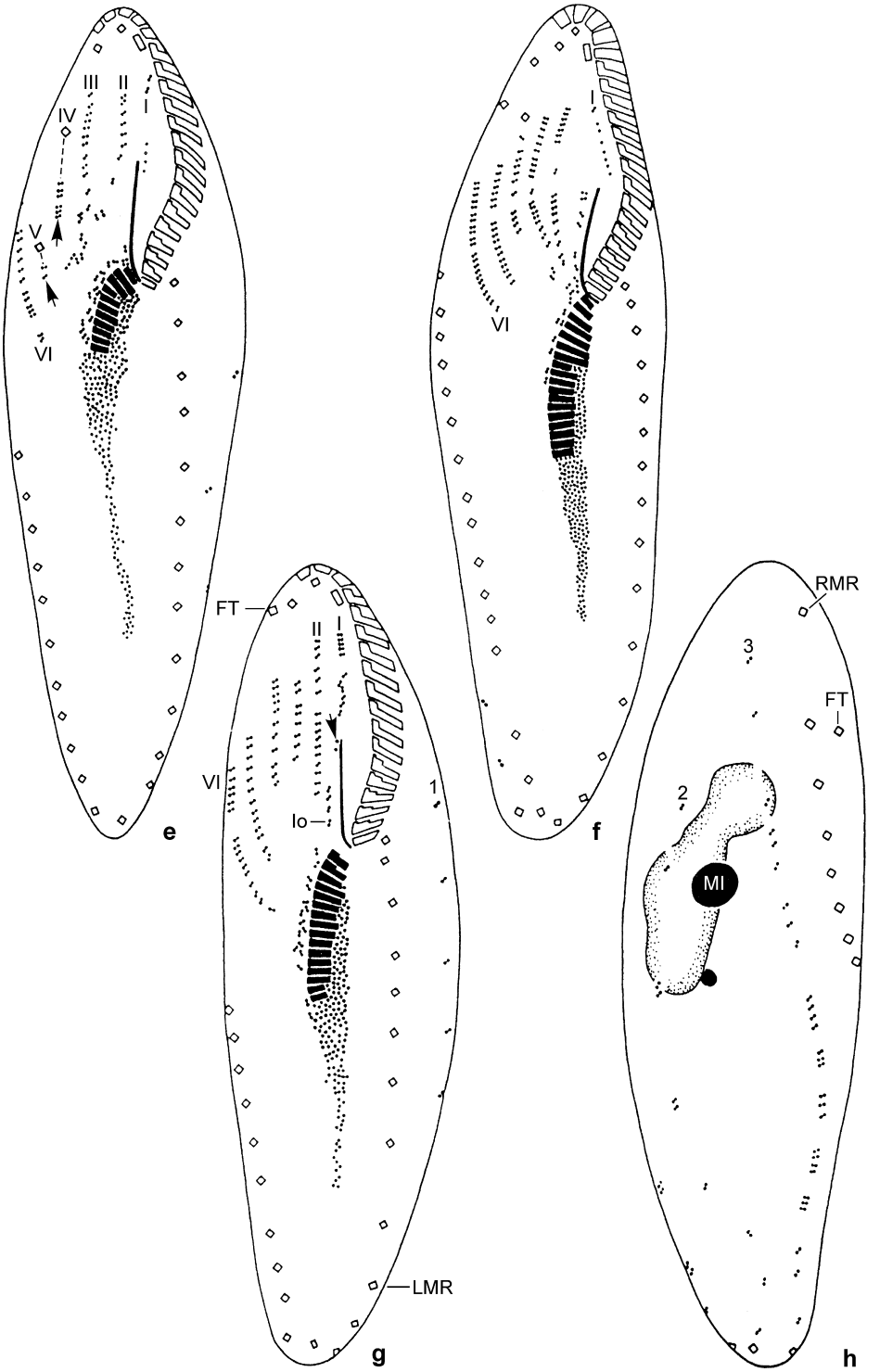
Gonostomum algicola can be separated from the congeners by the following features (Foissner et al. 2002a): (i) shorter adoral zone of membranelles (37% of body length on average vs. around 50%); (ii) slender body (4:1 vs. 2.6–3.4:1; Table 14); (iii) fine cirri (4 cilia vs. ≥8); (iv) low number of transverse cirri (1 vs. usually 3 or more); and (v) minute paroral (4 cilia vs. ≥10). However, the very short paroral is obviously the most important feature for the identification of the present species because *G. affine* from Saudi Arabia has, like G. *algicola*, only a single transverse cirrus (Fig. 12e), whereas the paroral of this population is composed of 5–14, on average 11 cilia which agrees very well with the values from the other "true" *G. affine* populations (Table 14). *Gonostomum namibiense*, which often also has a very short paroral (Fig. 22e, f) and sometimes also a rather low number of transverse cirri (Fig. 22h, Table 14), has a distinct tail and therefore cannot be confused with *G. algicola*.

Morphology: At first the neotype population studied by Foissner et al. (2002a) is described. The original description is in Hungarian and was not translated in detail. For some notes on the population described by Gellért (1942), see figure legend (Fig. 17a, b).

Body size of neotype specimens 60–110 × 15–30 µm in life[1]; length:width ratio also highly variable, namely 2.6–5.9:1, usually 3.9:1 both in life and after protargol impregnation. Body very flexible, but acontractile; dorsoventrally flattened up to 1.5:1. Body outline usually lanceolate, that is, distinctly tapering anteriorly and posteriorly, left margin almost straight, dorsal convex and with distinct furrow along anterior portion of right marginal row, which extends onto dorsal side; rarely elongate ellipsoidal or sigmoidal with bluntly pointed left anterior end (Fig. 18a, h–l). Macronuclear nodules usually slightly diagonal in central body portion, that is, anterior nodule in midline, posterior left of midline; elongate ellipsoidal, contain numerous globular chromatin bodies. Micronuclei near or attached to macronuclear nodules, globular, rarely ellipsoidal. Contractile vacuole slightly ahead of mid-body close to left cell margin, two collecting canals extending anteriorly and posteriorly. Cortical granules 0.8 × 0.5 µm in life, although highly refractive difficult to recognise because colourless and loosely spaced in longitudinal rows (Fig. 18n), stain red with methyl green-pyronin; tightly underneath cortex ellipsoidal structures, possibly mitochondria (Fig. 18m). Cytoplasm without crystalline inclusions, but with some colourless fat globules 2–3 µm across and about 5 µm-sized food vacuoles.

Adoral zone occupies about 37% of body length (about 50% in congeners; Table 14), commences near midline of anterior end of cell and extends straight along left body margin, performing abrupt right bend and slight counter clockwise rotation to plunge into buccal cavity near left body margin. Largest membranelle bases 4–5 µm wide, structure of membranelle depends on region (Fig. 18b): buccal membranelles composed of two long rows of basal bodies with, except for proximal-most mem-

[1] Calculated from measurements of live specimens and values given in Table 14, assuming a shrinkage of 10–20% due to the preparation procedures (Foissner et al. 2002a).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branelle, two short rows of unequal length attached at right anterior end; membranelles in middle portion of zone consist of two long rows of basal bodies and two very short rows each composed of two basal bodies; frontal membranelles very likely composed of 3–4 fairly short rows. Proximal portion of zone and buccal cavity covered by about 5 µm wide cortical process (buccal lip). Buccal cavity narrow and flat, at right bordered by slightly curved endoral composed of closely spaced basal bodies. Paroral slightly ahead and left of endoral, consists of only 3–6 widely spaced, about 9 µm long cilia. Pharyngeal fibres clearly recognisable only in protargol preparations, extend obliquely backwards (Fig. 18b, o).

Cirral pattern very constant, number of cirri of usual variability (Fig. 18b, o, Table 14). Cirri conspicuously fine compared to congeners because composed of only 2–8, usually four basal bodies (Fig. 18b, o). Eleven frontal-ventral[1] cirri on average (three frontal cirri; one buccal cirrus; usually four frontoventral cirri; usually three "postoral" ventral cirri). Frontal cirri about 12 µm long, not distinctly enlarged, except for slightly posteriorly displaced cirrus I/1, which is, as is usual for *Gonostomum*, elongate because made of 2 × 4 cilia. Buccal cirrus slightly right and ahead of paroral. Frontoventral cirri III/2 and IV/3 and postoral ventral cirri arranged as in *G. affine* (cp. Fig. 3a and Fig. 18b); anteriormost postoral ventral cirrus (IV/2) about at level of buccal cirrus; rearmost postoral cirrus usually distinctly ahead of, occasionally at level of buccal vertex. Frontoterminal cirri near or on dorsolateral surface, form short, slightly oblique row. Transverse cirrus at or slightly right of midline near posterior end of cell and therefore between rear end of marginal rows. Right marginal row commences dorsally at about 10% of body length in neotype specimen, terminates slightly more anteriorly than left row which commences left of proximal end of adoral zone (Fig. 18b, o, 19a–e); gap between rear end of marginal rows occupied by transverse cirrus on ventral side and caudal cirri on dorsal side; marginal cirri about 10 µm long in life.

← **Fig. 19e–h** *Gonostomum algicola* (from Foissner et al. 2002a. Protargol impregnation). **e:** Infraciliature of early divider, 74 µm. Anlagen IV and V are generated by the posteriormost cirrus of rows IV and V (arrows). The undulating membrane anlage separates at the right margin of the oral primordium. **f:** Infraciliature of early divider, 76 µm. Maturation of the adoral zone of membranelles and growth of anlagen IV and V, which probably incorporate the remaining frontoventral cirri, except for the frontal and frontoterminal cirri. **g, h:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen (69 µm) showing five primary primordia (anlagen II–VI) in the frontal area and intrakinetal proliferation of basal bodies in the dorsal kineties. Proter's anlage I originates from the parental paroral (arrow), while the opisthe's anlage I is generated by the oral primordium. The new frontal cirrus I/1, which is produced by the anlagen Ip and Io, assembles in the proter, while it still consists of widely spaced dikinetids in the opisthe. Note that the parental paroral (arrow), which is left of the endoral in morphostatic cells, moves to the right, very likely due to the flattening of the buccal cavity during the reorganisation of the parental oral apparatus (see also Fig. 19i). FT = frontoterminal cirri, LMR = left marginal row, MI = micronucleus, RMR = right marginal row, I–VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties (partially with anlagen). Page 116.

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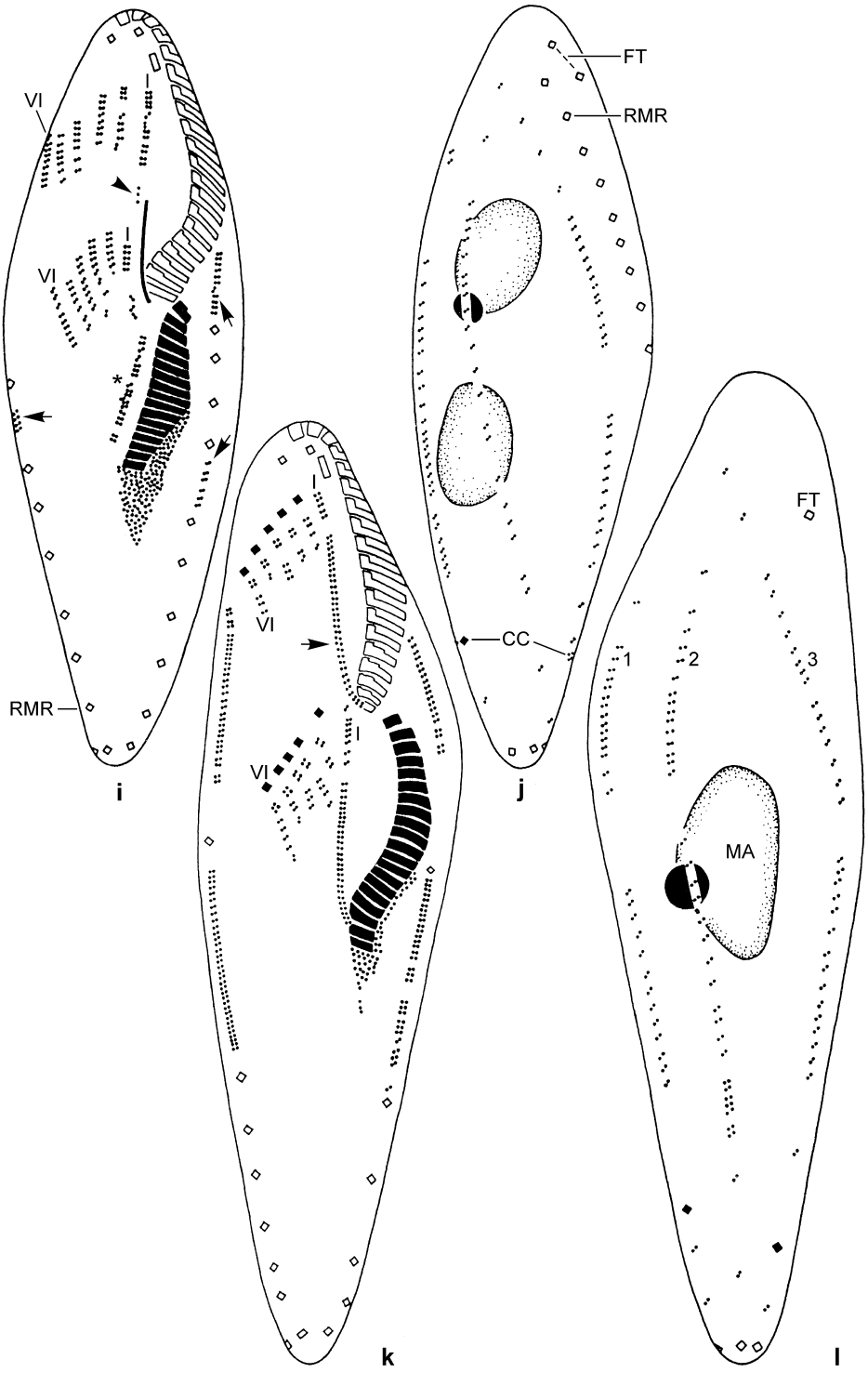
[1] Foissner et al. (2002a), par lapsus, wrote frontal-ventral-transverse cirri, although the single transverse cirrus in not included in these 11 cirri.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Dorsal bristles about 3 µm long in life, arranged in three more or less bipolar kineties (Fig. 18c, p). Kinety 1 extends along left cell margin, commences subapically at level of paroral; kinety 2 extends in double-curved line from left subapical end to centre (or somewhat right of it) of posterior body end; kinety 3 curves from centre of anterior end to right posterior body end. One caudal cirrus per kinety, right cirrus often on lateral surface near last marginal cirrus. Posterior marginal cirri, transverse cirrus, and caudal cirri difficult to distinguish in life and even in protargol preparations because of similar size and close together on narrowed body end; caudal cirri about 15 µm long in life.

Cell division (Fig. 18q–s, 19a–t, 20f, g, Table 15): Foissner et al. (2002a) studied the ontogenesis of *Gonostomum algicola* in great detail. As is usual for *Gonostomum* and some other genera, the cirral primordia II–VI are at first primary primordia (Foissner 1983a), which split into the secondary primordia only in middle dividers, that is, a distinction between proter's and opisthe's anlagen is not possible in early dividers, except for anlage I, which develops independently and differently. However, most primary primordia are formed from two different anlagen (Table 15), likely homologous as in most other hypotrichs (for compilation, see Table 4 in Berger 1999).

Stomatogenesis: The formation of the oral primordium begins with the apokinetal proliferation of basal bodies behind the buccal vertex, where a cuneate anarchic field develops (Fig. 18q, r). The formation of membranelles commences at the left anterior end of the oral primordium (Fig. 19a, d). As is usual, membranelle formation proceeds posteriad, while the anlage for the opisthe's undulating membranes separates as a streak of loosely arranged basal bodies at the right anterior margin of the oral primordium (Fig. 19e–g). These basal bodies arrange to a straight line of dikinetids distinctly separated from the adoral zone, which curves leftwards so that a rather wide buccal field is formed (Fig. 19i, k). Later, when the shaping of the oral apparatus commences, the undulating membranes incline and move close to the rear half of the adoral zone. Thus, the buccal field narrows. The further differentiation of the undulating membrane anlagen proceeds as follows (Fig. 19k, m): the anterior

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← **Fig. 19i–l** *Gonostomum algicola* (from Foissner et al. 2002a. Protargol impregnation). Parental structures white, new black. **i, j:** Infraciliature of ventral and dorsal side of same specimen, 68 µm. The five primary primordia (see Fig. 19g) have split transversely to form five secondary primordia each in proter and opisthe. Arrowhead marks rest of parental paroral. The opisthe anlage I generates frontal cirrus I/1, and the basal bodies for the paroral and endoral anlage align (asterisk). Short streaks develop from dedifferentiated cirri at two sites in each marginal row (arrows). The dorsal kineties anlagen begin to split at mid-body and caudal cirri originate at their ends. **k, l:** Infraciliature of ventral and dorsal side and nuclear apparatus of middle divider, 80 µm. Cirri segregate posteriad from the six frontal-ventral-transverse cirri anlagen in proter and opisthe. Proter's paroral and endoral are reorganising (arrow). The parental paroral has been either resorbed or incorporated into the anlage, which consists of distinct dikinetids. The macronuclear nodules fused to a globular mass. Note that caudal cirri are formed only at kineties 1 and 3 of opisthe at this stage; the other caudal cirri are formed later. CC = new caudal cirri, FT = frontoterminal cirri, MA = fused macronucleus, RMR = parental right marginal row, I, VI = frontal-ventral cirri anlagen, 1–3 = dorsal kineties. Page 116.

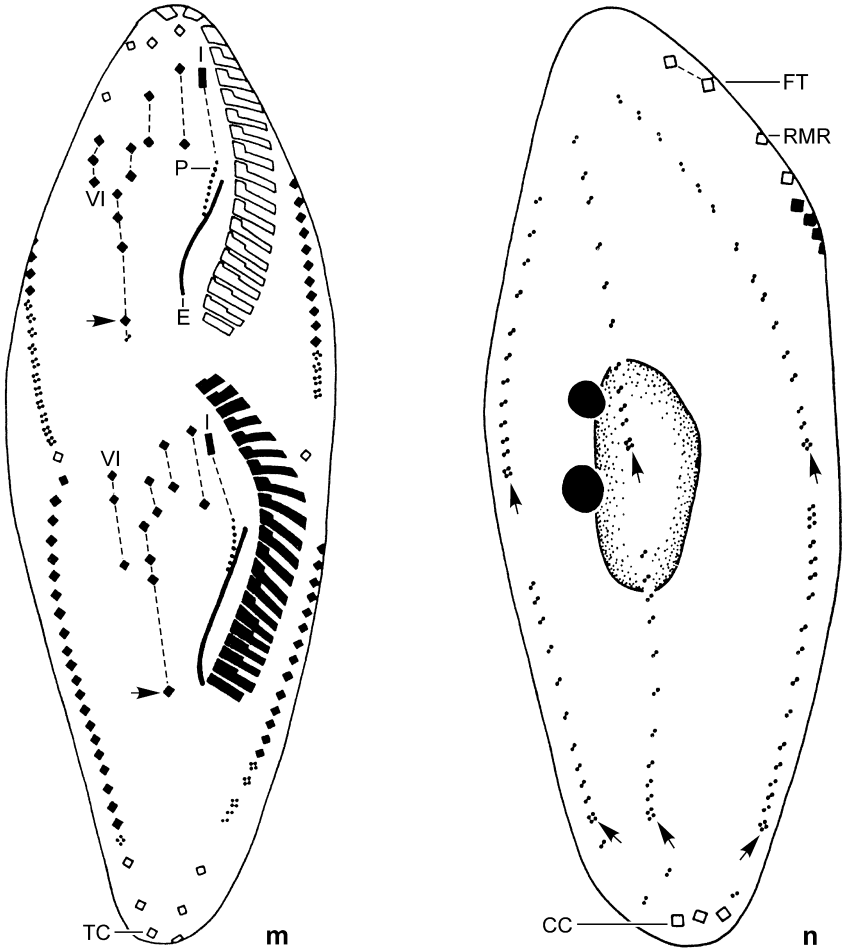


Fig. 19m, n *Gonostomum algicola* (from Foissner et al. 2002a. Protargol impregnation). **m:** Infraciliature of ventral side of late divider, 71 µm. Parental structures white, new black. The new cirri arrange to the mature pattern. Note that the single transverse cirrus (arrows) is formed by anlage V. **n:** Infraciliature of dorsal side and nuclear apparatus of late divider, 74 µm. Arrows mark new caudal cirri. E = endoral, FT = frontoterminal cirri, P = paroral, RMR = right marginal row, TC = transverse cirri, I, VI = frontal-ventral cirri anlagen. Page 116.

portion of the dikinetal line splits longitudinally, producing a long row of closely spaced basal bodies (the new endoral) to the left and a short row of widely spaced basal bodies (the future paroral) to the right. Interestingly and characteristic for the *Gonostomum*-group, the paroral locates left of the endoral when the buccal cavity is shaped, respectively, reorganised in the proter (Fig. 19m, o, q). Possibly, this is due to the growing buccal lip, which takes along the paroral. In the proter, both membranes reorganise after the formation of frontal cirrus I/1 (Fig. 19k, m), while the pa-

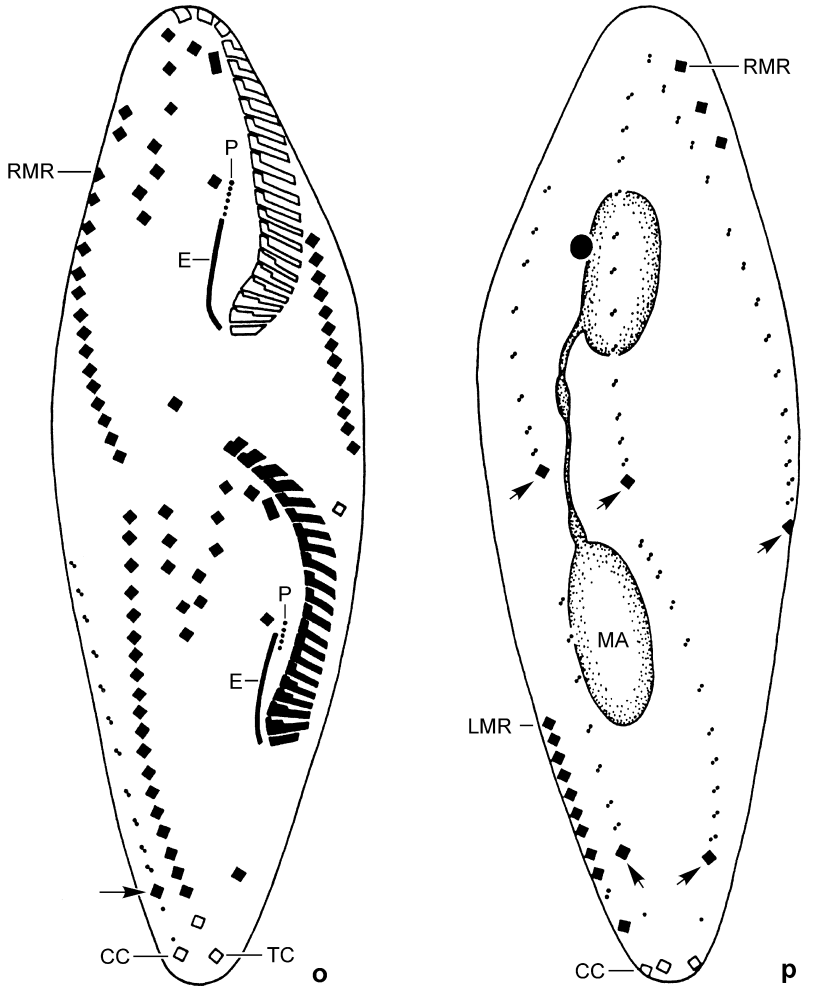


Fig. 19o, p *Gonostomum algicola* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral and dorsal side of late divider, 80 µm. Parental structures white, new black. Arrows mark new caudal cirri. Note that the paroral of the opisthe is already left of the endoral, likely due to shaping of opisthe's buccal cavity and lip, while that of the proter is still moving to the left. CC = parental caudal cirri, E = endoral, LMR = anterior end of left marginal row of opisthe, MA = macronuclear nodule, P = paroral, RMR = new right marginal row of proter, TC = parental transverse cirrus. Page 116.

rental adoral zone is retained; the pharyngeal fibres, however, disaggregate in middle dividers and are rebuilt in postdividers.

Frontal-ventral-transverse cirri: When the anarchic field of the oral primordium elongates, anlage I of the proter originates at (close to, that is, de novo?) the anterior end of the paroral, and the buccal cirrus disorganises and proliferates basal bodies anteriorly and posteriorly; furthermore, cirrus III/2 (= parabuccal cirrus) disorgan-

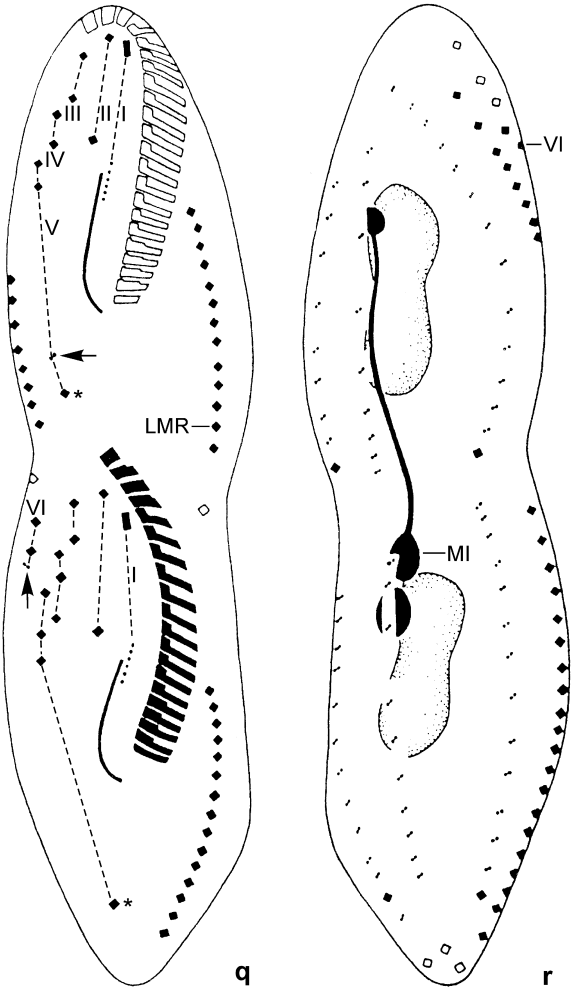


Fig. 19q, r *Gonostomum algicola* (from Foissner et al. 2002. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of late divider, 73 µm. Cirri originating from same anlage connected by broken line. The new paroral membranes are now left of the endoral in both filial products. Arrows mark kinetids which will be resorbed. Asterisks denote new transverse cirri. Parental structures white, new black. LMR = left marginal row of proter, MI = dividing micronucleus, I–VI = frontal-ventral-transverse cirri anlagen. Page 116.

ises and proliferates basal bodies posteriorly to form anlage III (Fig. 18r, s). Simultaneously, anlage VI is formed de novo right of and at large distance from the frontoterminal cirri (Fig. 18s). The parental frontoterminal cirri are, as is usual, not involved in primordia formation. Next, basal bodies from the anterior end of the oral primordium migrate anteriad and form two streaks right of the parental endoral (Fig. 19a, c, d): the left streak, which becomes opisthe's anlage I, is slightly but clearly separate from anlage II, while the right streak touches proter's anlage III. Subsequently, anlagen IV and V, which are generated by the posteriormost cirrus of parental rows IV and V (Fig. 19e), elongate anteriad, probably incorporating the remaining frontoventral cirri (Fig. 19f). Thus, two short anlagen (Ip and Io, which later form the new left frontal cirrus of proter and opisthe) and five long streaks (anlagen II–VI) are now recognisable in the frontal area. The long anlagen (= primary

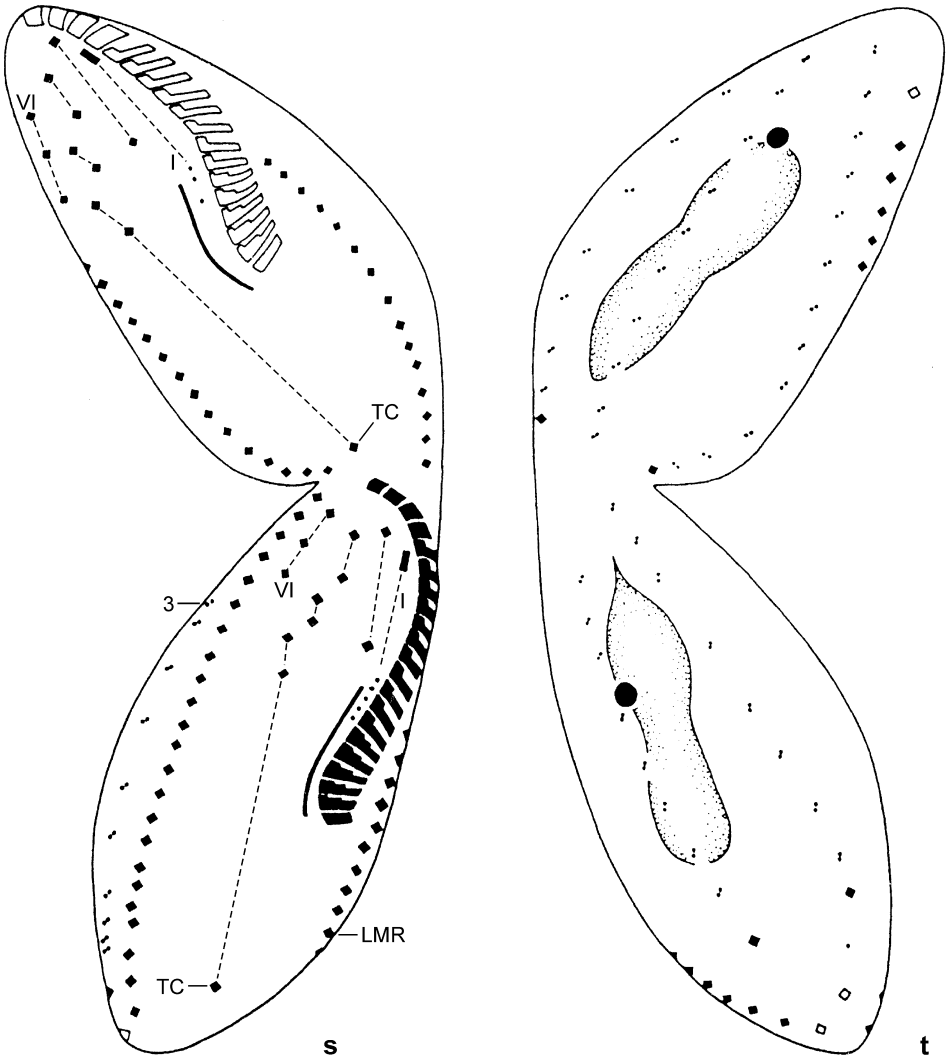


Fig. 19s, t *Gonostomum algicola* (from Foissner et al. 2002. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of very late divider, 68 µm. Note the low number of paroral cilia and the single transverse cirrus originating from anlage V. Cirri originating from same anlage connected by broken line. Parental structures white, new black. LMR = left marginal row of opisthe, TC = transverse cirrus, I, VI = frontal-ventral-transverse cirri anlagen, 3 = rightmost dorsal kinety (= kinety 3). Page 116.

primordia) then divide transversely to form a set of anlagen (= secondary primordia) each for the proter and the opisthe (Fig. 19f, g, i). Cirri segregate from anterior to posterior and very likely originate in the following, ordinary manner (Fig. 19k, m, o,

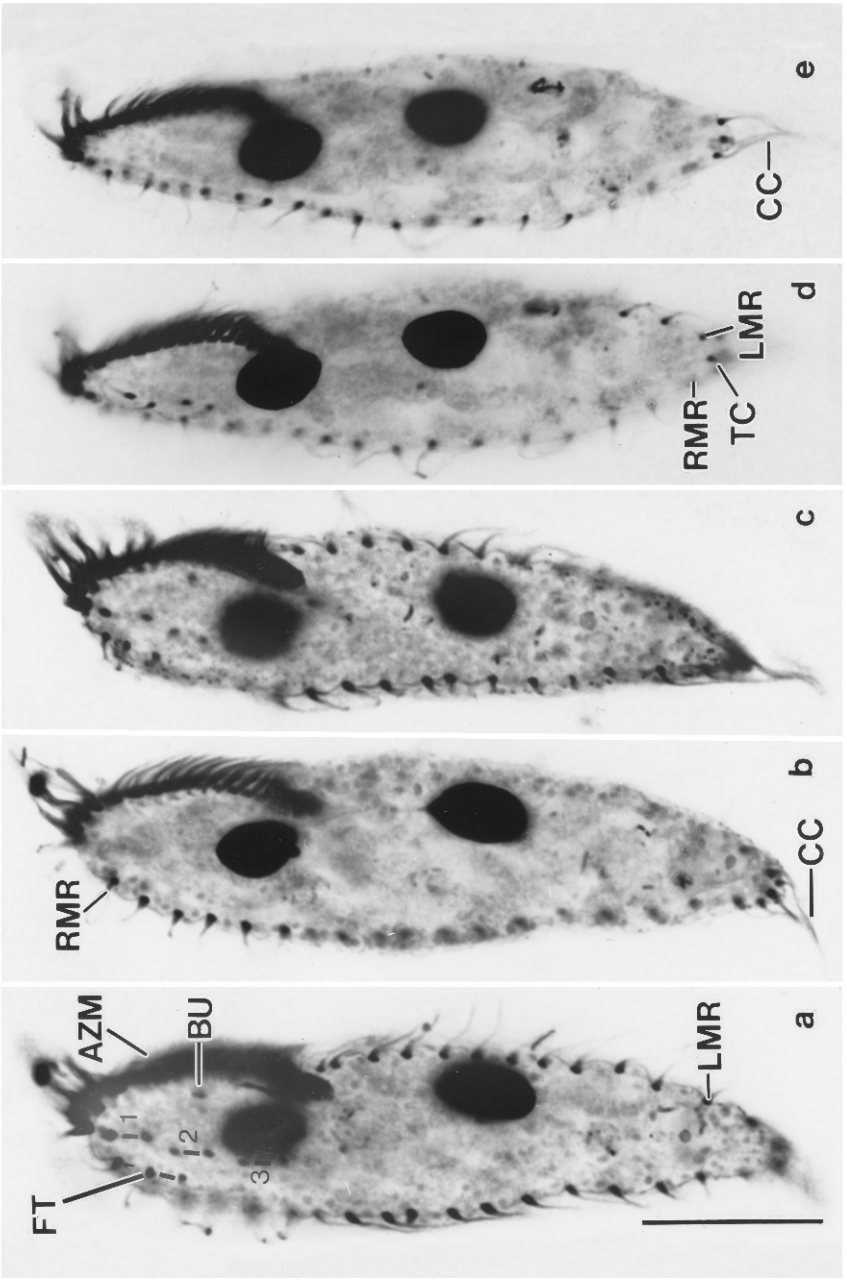


Fig. 20a–e *Gonostomum algicola* (from Foissner et al. 2002b. Protargol impregnation). Ventral views of three specimens at different focal planes (a and b; c; d and e) showing infraciliature and nuclear apparatus. This species is characterised, inter alia, by a lanceolate body outline, an adoral zone occupying only about 37% of body length (50% in most congeners), and fine cirri. The rearmost marginal cirri, the single transverse cirrus, and the caudal cirri are very closely arranged due to the nar-

Legend continued on p. 133

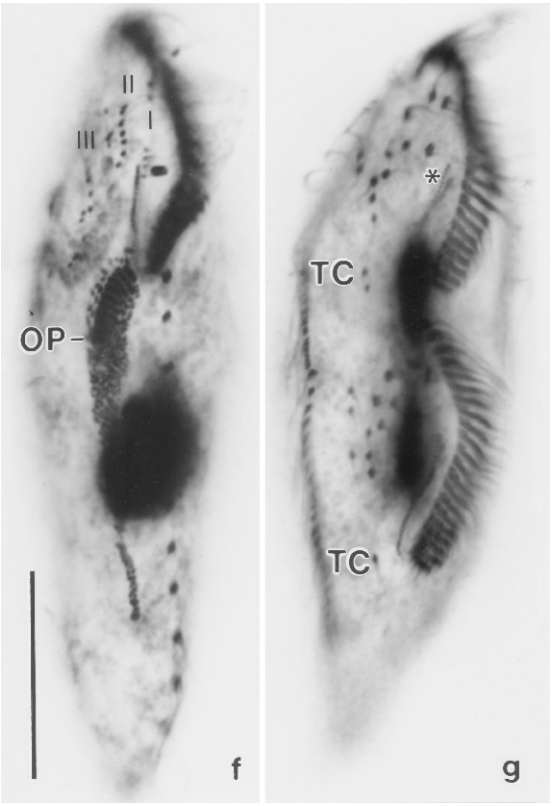


Fig. 20f, g *Gonostomum algicola* (from Foissner et al. 2002b. Protargol impregnation). **f:** Early divider in ventral view. Proter's anlage I originates from the parental paroral, while the buccal cirrus disorganises and proliferates basal bodies anteriorly and posteriorly becoming anlage II. Anlage III is formed by the parabuccal cirrus (cirrus III/2). For a more detailed explanation of the origin of the frontal-ventral-transverse cirri anlagen, see Table 15. **g:** Late divider in ventral view. The formation of membranelles in opisthe's adoral zone is complete. The new cirri migrate to their final positions. The anterior third (asterisk) of the undulating membranes anlagen splits longitudinally: the right part becomes the short paroral, the left becomes the long endoral; later, the paroral "migrates" to the left side of the endoral. Explanation of original labelling: I–III = frontal-ventral-cirri anlagen, OP = oral primordium, TC = transverse cirrus. Bar = 20 µm. Page 116.

Table 15): frontal cirrus I/1 (= left frontal cirrus) from anlage I; buccal cirrus (II/2) and frontal cirrus II/3[1] (= middle frontal cirrus) from anlage II; frontal cirrus III/3 (= right frontal cirrus) and cirrus III/2 from anlage III; (usually) one frontoventral cirrus (IV/3) and one "postoral" ventral cirrus (IV/2) from anlage IV; one transverse cirrus (V/1) and usually two postoral ventral cirri (V/2, V/3) from anlage V; two (cirri VI/3, VI/4) or three frontoterminal cirri from anlage VI. From the dividers shown in Fig. 19m, o, q it is clear that there exists some variability in the number of cirri formed from anlagen III–VI. Finally, the new cirri arrange to the mature pattern and replace the parental frontal cirri and frontoterminal cirri in the proter and the

← rowed body end and are thus difficult to distinguish, even in protargol preparations. Explanation of original labelling: AZM = adoral zone of membranelles, BU = buccal cirrus, CC = caudal cirri, FT = frontoterminal cirri, LMR = left marginal row, RMR = right marginal row, TC = transverse cirrus, 1–3 = cirral row/anlage III–V. Bar = 20 µm. Page 116.

[1] Note that Foissner et al. (2002, p. 805) designated the middle and right frontal cirrus "incorrectly" as cirrus II/1 and III/1. For correct designation (according to Wallengren 1900) of all cirri in the 18-cirri pattern, see Fig. 2a or Berger (1999, Fig. 6a).

transverse cirrus in the opisthe (Fig. 19q, s). The anlagen I–VI produce the following number of cirri: 1; 2; 2–3; 2–3, 3–4; 2–3.

The marginal rows, the dorsal kineties, and the nuclear apparatus divide as in congeners (for review, see Berger 1999). The marginal rows and dorsal kineties form an anlage each in the proter and the opisthe by intrakinetal proliferation of basal bodies; however, in the dorsal kineties these anlagen are only slightly separated from each other (Fig. 19i, k, m). Usually the caudal cirri are generated in a very specific time sequence: middle dividers produce a caudal cirrus each in kineties 1 and 3 of the opisthe (Fig. 19j, l), late dividers generate a caudal cirrus in the middle row of the opisthe and in each row of the proter (Fig. 19l, n). Occasionally, very late dividers produce caudal cirri only in rows 1 and 3 of the proter and in the middle row of the opisthe, while the caudal cirrus of proter's middle row only assembles in early postdividers (Fig. 19j, l, n). Other timings are also somewhat variable. For example, the macronuclear nodules may fuse before or after the primary primordia have split (Fig. 19g, h, k, l) and anlage I of the opisthe may develop at the beginning or after streak formation (Fig. 19a–f).

Foissner et al. (2002a) focused their studies on the formation of the frontal-ventral-transverse cirri anlagen, especially anlage VI, because previous results in congeners differ in this respect. They also studied an Australian population of *Gonostomum strenuum* (data not shown) which virtually has the same pattern as *G. algicola*.

Occurrence and ecology: *Gonostomum algicola* is likely confined to terrestrial habitats; so far reliable recorded only from Europe and Africa. Gellért (1942) discovered it in the algal layer of rocks and trees in Hungary; I checked the German papers by Gellért, but found no information about the locality.

Due to the neotypification by Foissner et al. (2002a), the new type locality is now in Namibia, where we found it in the thorn-bush girdle of the Etosha National Park-lookout site "Pan" (19°10'S 15°55'E), about 1 km off pan margin. The soil was grey and dusty and contained little litter and humus (further details, see Foissner et al. 2002a, p. 28, site 62). Further, Foissner et al. (2002a) found *G. algicola* in soil from alluvial grassland (dark, very humic, much litter and grass roots; pH 6.7) in the *Colophospermum mopane* forest surrounding the Bambatsi Guest Farm between the towns of Khorixas and Outju, 1150 m above sea-level (20°10'S 15°25'E; details see site 50 in Foissner et al. 2002a, p. 25). Further records: flood plain soils from two natural forest stands in eastern Austria (Müllerboden, *Pruno-Fraxinetum*; Beugenau, *Fraxino-Populateum*; Foissner et al. 2005, p. 627); beaches of Cantabrian Sea (Atlantic Ocean), Spain (Fernandez-Leborans 2000; p. 416).

Gonostomum algicola feeds on bacteria and their spores (Foissner et al. 2002a), but also on flagellates and algae (Gellért 1942).

Gonostomum albicarpathicum Vd'ačný & Tirjaková, 2006
(Fig. 21a–j, Table 14)

2006 ***Gonostomum albicarpathicum* nov. spec.**[1] – Vd'ačný & Tirjaková, Europ. J. Protistol., 42: 92, Fig. 1–12, Table 1 (Fig. 21a–j; original description; one holotype slide and four paratype slides are deposited in the Department of Zoology, Faculty of Natural Sciences of Comenius University in Bratislava, Slovakia).

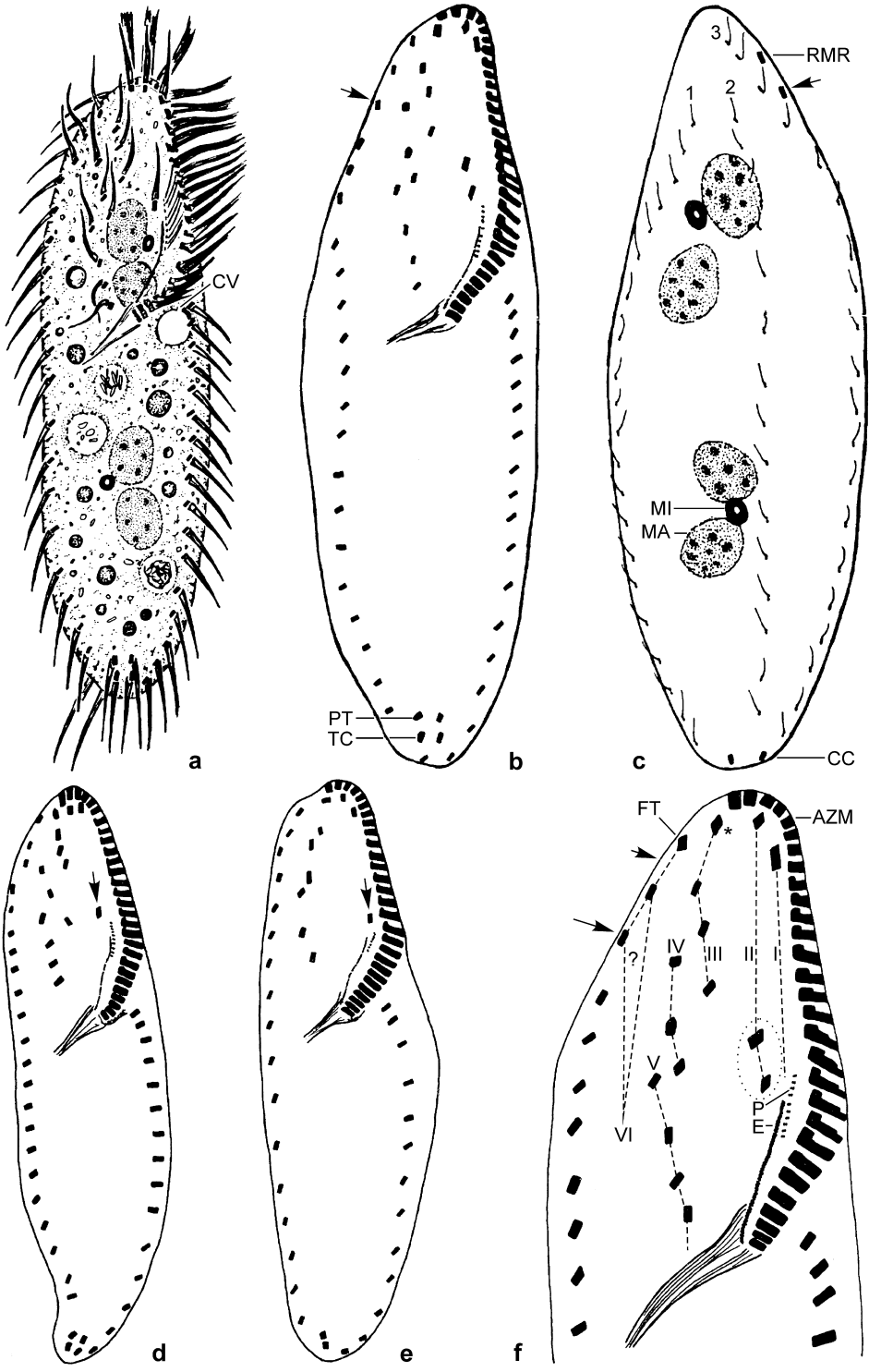
Nomenclature: The species-group name *albicarpathicum* is a composite of the Latin words *albus* (white, bright) and *carpathicus* (living in the Carpathian), referring to the site (White Carpathian Mountains) where the species was discovered (Vd'ačný & Tirjaková 2006a).

Remarks: The original description is very detailed. In spite of that it contains some uncertainties, namely, the number of buccal cirri, the number of frontoterminal cirri, and the relationship of the caudal cirri to the dorsal kineties. The authors studied 10 specimens in protargol preparations and found that five of them had two buccal cirri (Fig. 21b, f). According to Vd'ačný & Tirjaková (2006a), the anterior one could also be a frontoventral cirrus. However, this is unlikely because in that case it had to originate from anlage III whose cirral row runs about in the midline of the cell and is therefore distinctly separated from this buccal cirrus (Fig. 21f). Vd'ačný & Tirjaková (2006a) counted invariable three frontoterminal cirri, but according to Fig. 21f it cannot be excluded that the rearmost frontoterminal cirrus is a right marginal cirrus because the marginal row is difficult to distinguish from the frontoterminal cirri (Fig. 11, 12 in Vd'ačný & Tirjaková 2006a); perhaps the different distances between the frontoterminal cirri (see morphology for detailed explanation) is a result of this misinterpretation. When the rearmost cirrus of the three frontoterminal cirri would be in fact a frontoterminal then the right marginal row would have a distinct break between the second and third cirrus (Fig. 21b, c).

According to the original description, the two caudal cirri are likely related to dorsal kineties 2 and 3. Ontogenetic data are needed to make an ultimate decision for all three features discussed. In addition, *Gonostomum albicarpathicum* should be redescribed to check the stability of some features, for example, the number of macronuclear nodules, buccal cirri, frontoterminal cirri, and caudal cirri.

Obviously, the number of macronuclear nodules is the best feature to separate *G. albicarpathicum* from the congeners: 3–6, usually four in two pairs in the present species against 10–17, usually 14 in *G. kuehnelti* and two in all other species. The other separating characteristics discussed by Vd'ačný & Tirjaková (2006a), namely,

[1] Vd'ačný & Tirjaková (2006a) provided the following diagnosis: Body size about 70 × 22 µm in vivo; body outline elongate elliptical. Typically 4 macronuclear nodules, and on average 16 right marginal, 18 left marginal, 3 frontoterminal, 1–10 (on average 9) frontoventral cirri; frontoterminal cirri and frontoventral cirral rows not distinctly separate, the latter extending back as far as posterior end of adoral zone of membranelles; 1–2 buccal cirri at anterior end of paroral membrane composed usually of 9 kinetids; usually 2 transverse and 2 pretransverse ventral cirri forming a square pattern; 2 caudal cirri; 3 dorsal ciliary rows. Adoral zone of membranelles about 42% of body length, composed of 25 membranelles on average.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f

number of frontoterminal cirri, caudal cirri, and buccal cirri, should be checked in further populations and are fraught with problems because in other species the number of these cirri is somewhat variable; for example, *Gonostomum affine* from the Tullnerfeld area (Austria) has sometimes only two caudal cirri (Table 23 in Berger 1999) and *G. algicola* has two or three frontoterminal cirri (Fig. 18b, o).

Morphology: Body size 55–95 × 17–30 µm in life, on average about 70 × 22 µm; length:width ratio 2.9–3.6:1 in life, 3.3:1 on average after protargol impregnation. Body outline elongate elliptical with anterior end narrowly rounded; posterior end somewhat broader rounded (Fig. 21a). Body dorsoventrally flattened up to 2:1, sometimes slightly twisted about main body axis. Number and arrangement of macronuclear nodules rather variable: usually four nodules forming two pairs roughly in midline of cell; anterior pair about at level of posterior portion of adoral zone, posterior pair close to mid-body; in specimens with three or six nodules they form a strand slightly left of cell's midline; individual nodules usually elongate ellipsoidal, rarely globular or irregular, contain small to medium-sized chromatin bodies. Distance between pairs of nodules varies from 0.0–12.5 µm (Table 14). Of 43 specimens studied in life, 34 (= 79%) had four nodules (Fig. 21c, i, j), one had only three nodules (Fig. 21h), and eight specimens had six nodules (Fig. 21g); no specimen with five nodules was found. Number of micronuclei variable; especially in individuals with three or six macronuclear nodules. Usually one micronucleus near or attached to anterior and posterior macronuclear pair; rarely two or three micronuclei attached to one pair and one micronucleus attached to the other pair (Fig. 21c, g–j); individual micronuclei about 2.4 µm across in protargol preparations (Table 14). Contractile vacuole somewhat left of buccal vertex, during diastole with two collecting canals. Cortical granules lacking, or perhaps not distinguishable because colourless and minute (Vd'ačný & Tirjaková 2006a). Cytoplasm colourless, with few ordinary crystals (about 3 µm), some lipid droplets 1–4 µm across, and food vacuoles

← **Fig. 21a–f** *Gonostomum albicarpathicum* (from Vd'ačný & Tirjaková 2006. a, from life; b–f, protargol impregnation). **a:** Ventral view of a representative specimen, 76 µm. Note the four macronuclear nodules which are pair-wise arranged ahead of and behind mid-body. **b, c, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 75 µm. Note that the position of the right frontal cirrus (asterisk in f) is not identical in (b) and (f), indicating that the authors made two separate illustrations of the holotype specimen or they designated two holotypes. Perhaps the "frontoterminal" cirrus marked with an arrow (b) is the second right marginal cirrus (arrow in c). Long arrow in (f) marks rearmost frontoterminal cirrus; the question mark indicates that this cirrus could also be a right marginal cirrus (details, see text; ontogenetic data needed); short arrow marks slightly enlarged distance between first and second frontoterminal cirrus. Broken lines connect cirri which very likely originate from the same anlage (proposal has to be checked by ontogenetic data). The left frontal cirrus is, as is usual for *Gonostomum*, slightly larger and more posteriorly than the other two frontal cirri. Note that in the original description, the dorsal kinety pattern is shown from the ventral side (Fig. 3 in Vd'ačný & Tirjaková 2006). **d, e:** Variability of cirral pattern. Arrows mark single buccal cirrus (vs. two in holotype). AZM = adoral zone of membranelles, CC = caudal cirri, CV = contractile vacuole, E = endoral, FT = anteriormost frontoterminal cirrus, MA = rearmost macronuclear nodule, MI = micronucleus, P = paroral, PT = pretransverse ventral cirri (originate from anlage V and VI), RMR = right marginal row, TC = transverse cirri, I–VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 135.

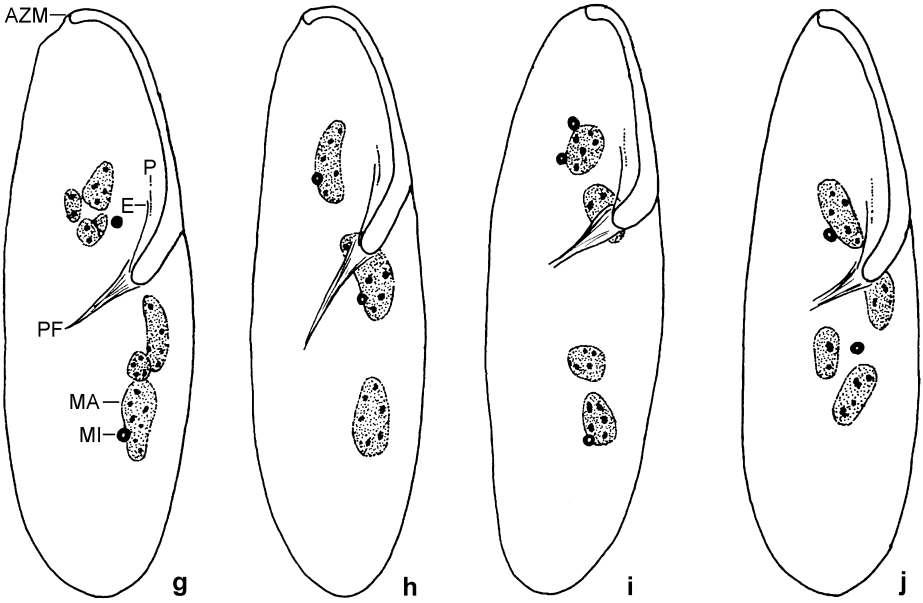


Fig. 21g–j *Gonostomum albicarpathicum* (from Vd'ačný & Tirjaková 2006. Method not indicated, likely after protargol impregnation). Ventral views showing variability of body outline and nuclear apparatus. AZM = adoral zone of membranelles, E = endoral, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres. Page 135.

4–5 µm in diameter. Movement inconspicuous, that is, glides slowly to rather rapidly on microscope slide.

Oral apparatus in *Gonostomum*-pattern (see genus section and Berger 1999). Adoral zone occupies 42% of body length and composed of 25 membranelles on average (Fig. 21a, b, Table 14). Bases of largest membranelles about 5 µm wide, cilia about 9 µm long. Buccal cavity narrow and flat. Paroral commences somewhat behind level of rearmost buccal cirrus, composed of 9–12 widely spaced, at least 5 µm long cilia. Endoral begins about at half length of paroral, more or less straight, terminates close to proximal-most adoral membranelle, composed of tightly spaced, on average 10 µm long cilia. Pharyngeal fibres clearly recognisable in life and protargol preparations, extend obliquely backwards.

Cirral pattern rather constant, number of cirri of usual variability (Fig. 21a, b, d–f, Table 14). Frontal cirri about 11 µm long, arranged in *Gonostomum*-pattern, that is, left cirrus (I/1) slightly enlarged and distinctly behind level of middle (II/3) and right cirrus (III/3)[1]. 1–2 buccal cirri somewhat right of anterior end of paroral;

[1] Note that the authors provided two illustrations of the ventral infraciliature of the holotype specimen (Fig. 2, 6 in Vd'ačný & Tirjaková 2006a [= Fig. 21b, f in present book]). Interestingly, they slightly differ, inter alia, in the arrangement of the cirri, for example, the right frontal cirrus (= cirrus III/3) and the cytopharynx. Thus, I suppose that they incorrectly fixed two specimens as holotype.

possibly one of these two cirri is a frontoventral cirrus (Vd'ačný & Tirjaková 2006a). Usually 6–10 frontoventral and "postoral" ventral cirri (frontoterminal cirri not included), arranged in three short, staggered rows and thus forming a rather irregular pattern usually terminating ahead of level of buccal vertex; anteriormost row likely originating from anlage III. Invariably three frontoterminal cirri near or on right dorsolateral surface (Fig. 21b, f, Table 14); distance between anteriormost and middle cirrus slightly greater than distance between middle and rearmost cirrus, a feature not clearly recognisable in the holotype specimen (Fig. 21b). According to Vd'ačný & Tirjaková (2006a) the frontoterminal and frontoventral cirri are not distinctly separated; likely this refers to the anterior end of both rows. According to Fig. 21b, e, f, the frontoterminal cirri are also difficult to distinguish from the anterior portion of the right marginal row; perhaps the "frontoterminal" cirrus marked with an arrow in Fig. 21b is the second right marginal cirrus (Fig. 21c, arrow). Usually two pretransverse ventral and two transverse cirri forming a square pattern; transverse cirri not enlarged (Fig. 21b). Right marginal row commences at about 6% of body length in holotype specimen, extends dorsolaterally anteriorly, terminates slightly ahead of level of transverse cirri. Left row begins left of proximal end of adoral zone, extends to posterior end of cell. Frontoventral and marginal cirri 8–9 µm long.

Dorsal bristles about 3 µm long, arranged in three kineties. Kineties 1 and 2 commence at about 15% of body length and terminate near rear cell end in holotype specimen (Fig. 21c); run close to left cell margin and in midline of cell, respectively. Kinety 3 of body length, extends along right body margin. One caudal cirrus each seem to be associated with kineties 2 and 3, easily distinguished from marginal cirri; caudal cirri about 11 µm long.

Occurrence and ecology: So far *Gonostomum albicarpathicum* is only recorded from the type locality, which is at Moravské Lieskové, Biele Karpaty (White Carpathian Mountains) in Slovakia, where Vd'ačný & Tirjaková (2006a) discovered it in soil mixed with leaf-litter (0–4 cm) from a Hornbeam forest (*Carpinus betulus*). It was rare and moderate abundance was achieved between third and fifth day after saturation of samples. According to Foissner (2007, p. 12), this quadrinucleate species is perhaps a local or Carpathian endemic since he did not find it in more than 1000 soil samples world-wide, including eastern Austria. Another possibility is that *G. albicarpathicum* is confined to *Carpinus betulus* forests, which are not anymore widely distributed in Europe (Ellenberg 1996). A similar phenomenon is known from *Territricha stramenticola* Berger & Foissner, 1988, which prefers or is even confined to litter of *Fagus sylvatica* (for review, see Berger 1999, p. 888).

Gonostomum albicarpathicum feeds on bacteria and their spores (Vd'ačný & Tirjaková 2006a).

Gonostomum namibiense Foissner, Agatha & Berger, 2002
(Fig. 22a–j, Table 14)

2002 ***Gonostomum namibiense* nov. spec.**[1] – Foissner, Agatha & Berger; Denisia, 5: 810, Fig. 176a–j, Table 156 (Fig. 22a–j; original description; the holotype slide [accession number 2002/121], one paratype slide [2002/122], and three voucher slides [2002/123, 124, 360] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; see also Aescht 2008, p. 168).

2004 ***Gonostomum namibiense* Foissner et al., 2002** – Foissner, Moon-van der Staay, van der Staay, Hackstein, Krautgartner & Berger, Europ. J. Protistol., 40: 267, 273, Fig. 5 (estimation of phylogenetic position using SSU rRNA; GenBank accession No.: AY498655).

Nomenclature: The species-group name refers to the country where the species was discovered (Foissner et al. 2002a).

Remarks: The present species differs from all congeners by the tail, a very distinct characteristic facilitating identification of live specimens. However, some further tailed, so far undescribed species are known to exist and therefore the identification has to be checked in protargol preparations (Foissner et al. 2002a). The tail of *G. namibiense* is very likely the result of a body elongation and not due to a narrowing of the (ordinary) rear body portion because the usual *Gonostomum* ratio of 50% of length of adoral zone:body length[2] is only obtained when the tail is omitted (Foissner et al. 2002a).

In life, *Gonostomum namibiense* is easily confused with tailed *Paragonostomum* species (see p. 172). However, they lack transverse cirri and cortical granules, and *P. multinucleatum* has a row of 4–9 (mean = 7) macronuclear nodules, while *P. caudatum* and *P. rarisetum* lack the frontoventral cirral pairs which are so distinct in the present species. Relevant molecular data of *Paragonostomum* species are needed to prove or disprove the generic assignment of *G. namibiense*. *Urosoma* species have postoral ventral cirri and only four frontoventral cirri (for review, see Berger 1999, p. 396).

Foissner et al. (2002a) found *G. namibiense* in several sites of Namibia (see occurrence and ecology). However, the populations from sites (30) (Fig. 22h, i, Table 14) and (49) (Fig. 22j) might be distinct subspecies because of considerable differences in quite a number of morphometrics. On the other hand, body shape, cortical granules, and cirral pattern are rather similar in all populations. Thus, further populations have to be studied morphologically, ontogenetically, and molecularbiologically to get a better insight into the systematics of this group. Comparable differ-

[1] Foissner et al. (2002a) provided the following diagnosis: Size about 90 × 20 µm in vivo. Elongate lanceolate with tail-like posterior portion occupying about 15% of body length, 2 macronuclear nodules. Cortical granules about 1 × 0.3 µm, colourless, scattered. On average 26 right marginal, 17 left marginal, 2 frontoterminal, 6 frontoventral, 2 pretransverse, and 5 transverse cirri; 1 buccal cirrus in front of anterior end of paroral. Adoral zone of membranelles about 37% of body length, composed of 27 membranelles on average. 5–10, usually 6 paroral kinetids.

[2] In Foissner et al. (2002a, p. 813) we erroneously wrote "... ratio of body length:length of adoral zone ...".

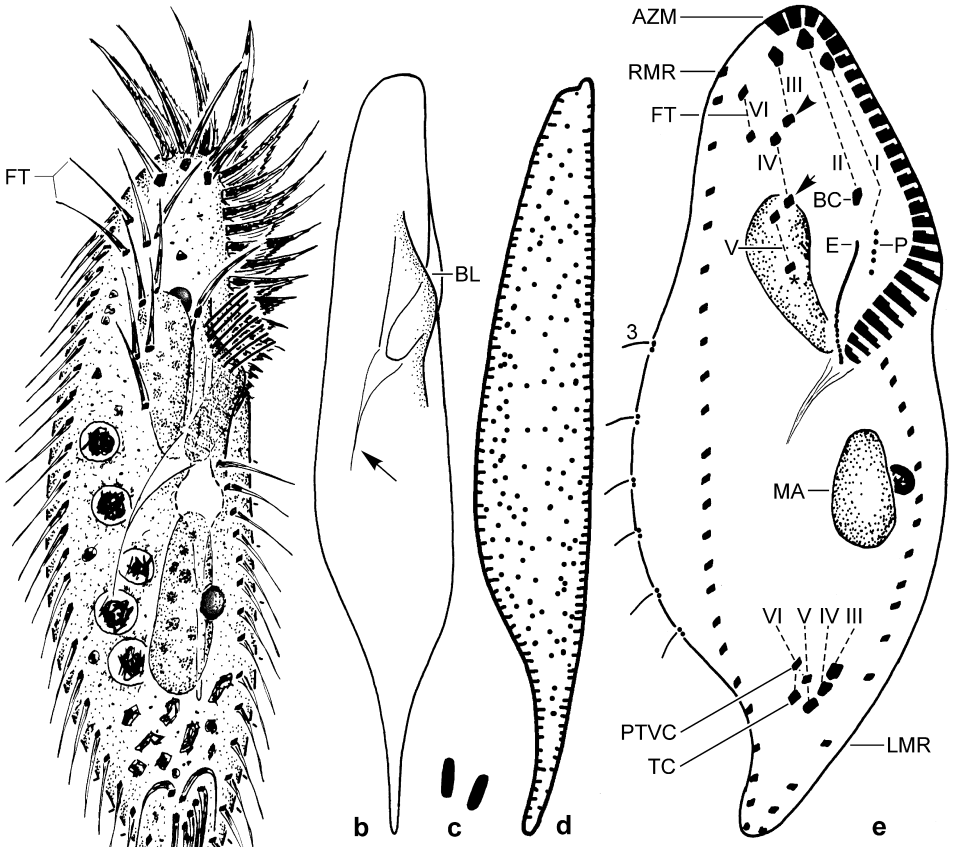
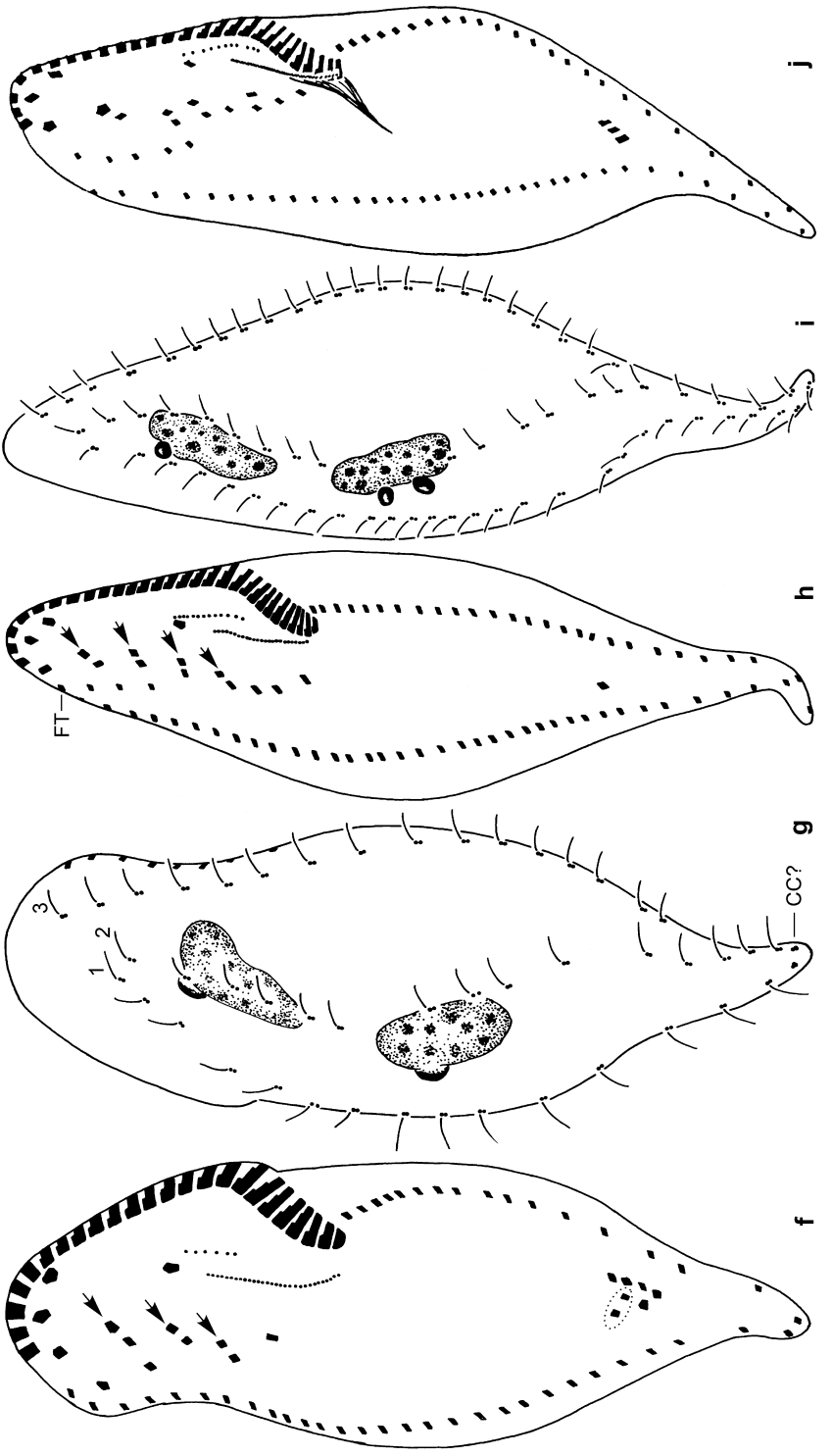


Fig. 22a–e *Gonostomum namibiense* (from Foissner et al. 2002a. a–d, from life; e, protargol impregnation). **a:** Ventral view of a representative specimen, 89 µm. **b:** Lanceolate shape variant showing large buccal lip. Arrow marks pharyngeal fibres. **c:** The cortical granules are colourless and about 1.0 × 0.3 µm in size. **d:** Right lateral view showing dorsoventral flattening and arrangement of cortical granules. **e:** Infraciliature of ventral side and nuclear apparatus of paratype specimen, 92 µm. Arrowhead and arrow mark pseudopairs; arrowhead marks cirrus III/2; arrow denotes cirrus IV/2, which forms, together with the two cirri of anlage V (rear cirrus marked with asterisk), the anteriorly displaced postoral ventral cirri. Frontal-ventral-transverse cirri which originated from the same anlage (I–VI) are connected by broken lines (proposal has to be confirmed or rejected by cell division data). Note that *G. namibiense* is an 18-cirri hypotrich; however, this specimen lacks the transverse cirrus formed by anlage II. AZM = distal end of adoral zone of membranelles, BC = buccal cirrus, E = endoral, FT = frontoterminal cirri, LMR = left marginal row, MA = macronuclear nodule (with attached micronucleus), P = paroral, PTVC = pretransverse ventral cirri (connected by dotted line), RMR = right marginal row, TC = transverse cirri, I–VI = frontal-ventral-transverse cirri anlagen, 3 = dorsal kinety 3. Page 140.

ences have been reported among *Gonostomum affine* populations (Berger 1999, Foissner et al. 2001).



Legend on p. 143

Some specimens of *G. namibiense* are real "18-cirri" hypotrichs, for example, that shown in Fig. 22e. Their cirral pattern rather clearly shows that it must have developed from the ordinary six anlagen I–VI. By contrast, a considerably part of the type population has more cirri forming more than two frontoventral cirral pairs (Fig. 22f). Such a pair-formation usually points towards an increased number of cirral anlagen, that is, seven (Fig. 22f) or even more (Fig. 22h). Of course, ontogenetic data are needed to confirm or disprove this assumption.

Morphology: Body size 80–110 × 15–25 µm in life, usually near 90 × 20 µm. Body elongate ellipsoidal or lanceolate, with short but distinct tail occupying about 15% of body length in life (Fig. 22a, b, d, Table 14). Cells acontractile, but flexible and very fragile, prepared specimens thus considerably stouter (2.8–3.5:1, on average 3.1:1) and with broadened tail. Trunk flattened dorsoventrally up to 2:1 and asymmetrical; left body margin straight to slightly sigmoidal, right margin distinctly S-shaped. Anterior macronuclear nodule about in, posterior slightly left of midline; nodules ellipsoidal (2:1) to elongate ellipsoidal (3:1), contain numerous globular chromatin bodies. Micronuclei near or attached to macronuclear nodules, about 3 µm across in life. Contractile vacuole near mid-body behind buccal vertex, during diastole with two collecting canals (Fig. 22a). Cortical granules closely spaced, scattered, difficult to recognise because minute (1.0 × 0.3 µm) and colourless, stain red with methyl green-pyronin and increase to 2 × 1 µm (Fig. 22c, d); impregnate more or less intensely with protargol. Cytoplasm colourless, but opaque, with 1–3 µm-sized crystals mainly in posterior body portion, and food vacuoles 4–5 µm across. Glides slowly to rather rapidly on microscope slide.

Oral apparatus in *Gonostomum* pattern (Fig. 22a, e, f). Adoral zone occupies only about 37% of body length (against about 50% in most congeners; Berger 1999), composed of 26 membranelles on average, commences near cell midline at anterior body end and extends straight along left body margin, performing abrupt bend and slight clockwise rotation to plunge into buccal cavity near left body margin. Largest membranelle bases about 5 µm wide. Proximal portion of adoral zone and buccal cavity almost entirely covered by curved, rather prominent cortical process (buccal lip) bearing paroral which is composed of 5–10 widely spaced, 10 µm long cilia. Buccal cavity flat and narrow, at right bordered by slightly curved endoral membrane composed of tightly spaced basal bodies. Pharyngeal fibres clearly recognisable in life, extend obliquely backwards.

← **Fig. 22f–j** *Gonostomum namibiense* (from Foissner et al. 2002a. Protargol impregnation). **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 70 µm. More detailed labelling see (e). Arrows mark cirral pairs. Pretransverse ventral cirri encircled. **h, i:** Infraciliature of ventral and dorsal side and nuclear apparatus of a specimen from Namibian site (30). This population is likely an own subspecies/species as indicated, inter alia, by the higher number of frontoterminal cirri, frontoventral cirri forming "midventral pairs", paroral cilia, and bristles per dorsal kinety, and a lower number of transverse cirri. Arrows mark cirral (pseudo)pairs. **j:** Ventral infraciliature of specimen from Namibian site (49). CC? = caudal cirri?, FT = frontoterminal cirri, 1–3 = dorsal kineties. Page 140.

In the present paragraph only the cirral pattern of the type population (Fig. 22e–g, Table 14) is described in detail (for pattern of other populations, see Fig. 22h–j, Table 14). Cirral pattern rather constant and conspicuous because of midventral-like frontoventral cirral pairs in many specimens; number of cirri of usual variability (Fig. 22e, f, Table 14). Most cirri abut 10 µm long. On average 6.4 cirri on frontal area[1] (Fig. 22f, Table 14; frontal cirri, buccal cirrus, and frontoterminal cirri not included. Of 18 specimens analysed morphometrically, five had five cirri, two had six cirri, 10 had seven cirri, and one had nine cirri). Frontal cirri moderately enlarged, form distinctly curved pseudorow. Buccal cirrus slightly right and in front of paroral. Frontoventral cirri arranged in 2–4, usually three pairs[2] and a single cirrus behind forming a "midventral" pattern slightly right of or in cell midline and not extending beyond level of buccal vertex (Fig. 22e, f); in holotype specimen terminating at 33% of body length (Fig. 22f). Usually two frontoterminal cirri left of anterior part of right marginal row. Usually two pretransverse ventral cirri close to transverse cirri. Transverse cirri subterminal in cell midline, form hook-like pattern, slightly enlarged, about 15 µm long in life. Right marginal row commences about at level of right frontal cirrus, extends roughly along body margin, and terminates – like left row – at tail tip where the cirri are almost cilia-like and thus easily mistaken for dorsal bristles. Left marginal row begins left of proximal end of adoral zone; distance between individual cirri often rather wide in tail-region.

Dorsal bristles 3–4 µm long in life, arranged in three rows (Fig. 22e, g): kinety 1 extends, except anteriorly, along left body margin, commences – like row 2 – at about 14% of body length in holotype specimen. Kinety 3 commences apically and extends along right cell margin. Possibly two fine caudal cirri at tail tip; however, the arrangement and composition of the tail ciliature are difficult to analyse because both (marginal? caudal?) cirri and dorsal bristles are composed of basal body pairs; in life, the bristles (cirri) on the tail tip are inconspicuous. Consequently, caudal cirri have not been included in the diagnosis by Foissner et al. (2002a). Ontogenetic data are needed to described the ciliature of this body region accurately.

Molecular data: The SSU rRNA of *G. namibiense* (population from Namibia, Etosha Pan, mud and soil from water hole Riedfontein) is 1773 base-pairs long (GenBank Accession No. AY498655; Berger et al. 2004, Foissner et al. 2004). The tree provided by Foissner et al. (2004) clearly shows that *G. namibiense* is more closely related to *G. strenuum* than to any other hypotrich, supporting the morphological classification based on the gonostomatid oral apparatus and the cirral pattern (postoral ventral cirri right of adoral zone, transverse cirri present). The next relative according to these molecular analyses is *Orthoamphisiella breviseries* (p. 642), followed by a group comprising *Engelmanniella mobilis*, *Hemiurosoma terricola*, *Ony-*

[1] In the original description we wrote that "12 frontoventral cirri" are present on average (Foissner et al. 2002a, p. 811); now I do not exactly recall how this number came about. Probably this number includes the frontal cirri (3), the buccal cirrus (1), three frontoterminal cirri (usually 2), and the 6.4 cirri mentioned above and in Table 14.

[2] Note that specimens with three or four pairs produced their frontoventral transverse cirri likely from more than six anlagen (assumption has to be confirmed by ontogenetic data).

chodromopsis flexilis, *Oxytricha granulifera*, and *Halteria*. Gong et al. (2006) found a close relationship between *G. namibiense* and *O. breviseries*, followed by *G. strenuum* and *Trachelostyla pediculiformis*. Shao et al. (2007) also found a close relationship of *Gonostomum*-species with *Orthoamphisiella*, *Hemiurosoma*, and *Trachelostyla* ((((((*G. namibiense* + *G. strenuum*) + *O. breviseries*) + *H. terricola*) + *T. pediculiformis*) + oxytrichids) + urostyloids). Chen et al. (2008, p. 577) isolated a population with 98% similarity in 18 SSU rRNA in Lake Taihu, a large shallow subtropical lake in the delta of the Yangtze River in Eastern China. In the tree published by Shao et al. (2008), the present species is the nearest relative to the urostyloids, which branch off at the base of the hypotrichs. According to Yi et al. (2009, their Fig. 2), *Gonostomum namibiense* is closely related to *Amphisiella magnigranulosa* (for review, see Berger 2008, p. 273, as *Uroleptoides magnigranulosus*) and *Orthoamphisiella breviseries* (Fig. 107a–k). In a tree recently published by Shao et al. (2010), *Gonostomum namibiense* is the sistergroup of the stylonychines, probably a distinct misclassification due to the low number (14) of hypotrichs used in this tree which is mainly dealing with the urostyloids. By contrast, Kim et al. (2010) found that *G. namibiense* and *G. strenuum* branch off at the base of the Hypotricha tree.

A sistergroup relationship of *G. namibiense* and *G. strenuum* is also demonstrated by Foissner & Stoeck (2006a, 2008; however, in both cases *O. breviseries* is distinctly separated), Schmidt et al. (2007; next relative is *Oxytricha saltans*), Li et al. (2008), Sonntag et al. (2008), Hu et al. (2009b), and in one tree published by Paiva et al. (2009, their Fig. 2), but not in another tree released in this paper (Paiva et al. 2009, their Fig. 1).

The results of the many molecular analyses are rather different, both in details and the general organisation. Only the following messages seem to be more or less correct: (i) *Gonostomum namibiense* and *G. strenuum* are closely related, as clearly indicated by their common position in *Gonostomum* based on the morphology; (ii) *Orthoamphisiella breviseries* is perhaps/likely a close relative of *Gonostomum*; (iii) *Gonostomum* is not an oxytrichid as supposed previously (Berger 1999), but branches off rather basal in the Hypotricha tree, confirming my more recent hypothesis that *Gonostomum* is a non-dorsomarginalian hypotrich (Berger 2008, p. 46).

Occurrence and ecology: *Gonostomum namibiense* is likely confined to terrestrial habitats. The type locality is the Etoscha National Park-lookout site "Pan" on the margin of the Etoscha Pan (19°10'S 15°55'E), Namibia (site 61 in Foissner et al. 2002a, p. 28). The sample was from a highly saline soil (40‰; pH 9.0) from a sedge girdle.

Further, we found it in four other sites in Namibia (Table 4 in Foissner et al. 2002a): site (30), soil from around a pond in the so-called, Riedloch, Aubschlucht (Fig. 22h, i; Table 14); site (49), soil from the Bambatsi Guest Farm between the towns Khorixas and Oujo (Fig. 22j); site (53), soil from a salt bush island near the Wolfsnes water-hole, Etosha National Park; and site (70), soil from salt-bush and grass girdle near the Okerfontein water-hole, Etosha National Park (more detailed descriptions of sites, see Foissner et al. 2002a). Foissner et al. (2002a) found *G. na-*

mibiense also in a slightly saline soil from Saudi Arabia, indicating that it has a wide geographical distribution and prefers saline habitats. Feeds likely mainly on bacteria (Foissner et al. 2002a).

Gonostomum strenuum (Engelmann, 1862) Sterki, 1878
(Fig. 13a, 23a–k, 24a–e, Tables 14, 15)

1862 ***Oxytricha strenua* n. sp.**[1] – Engelmann, Z. wiss. Zool., 11: 387, Tafel XXXI, Fig. 14 (Fig. 23a; original description; no type material available).

1878 ***Oxytricha strenua*** – Sterki, Z. wiss. Zool., 31: 57 (combination with *Gonostomum*; see nomenclature).

1882 ***Plagiotricha strenua*, Eng. sp.** – Kent, Manual infusoria II, p. 772, Plate XLIII, Fig. 34 (redrawing of Fig. 23a; combination with *Plagiotricha* Kent, 1882 and detailed revision of hypotrichs).

1888 ***Stichochaeta strenua* (Engelmann)** – Gourret & Roeser, Archs Biol., 8: 187 (combination with *Stichochaeta* Claparède & Lachmann, 1858).

1911 ***Gonostomum affine* (Stein)** – Goodey, Proc. R. Soc., 84: 169, Plate 4, fig. 9 (Fig. 118o in Berger 1999; very likely a misidentification).

1929 ***Gonostomum andoi*, sp. nov.** – Shibuya, Proc. imp. Acad. Japan, 5: 156, Text-fig. 2 (Fig. 23b; original description of new synonym; no formal diagnosis provided and likely no type material available).

1932 ***Gonostomum (Oxytricha) strenuum* (Engelmann, 1862)** – Kahl, Tierwelt Dtl., 25: 597, Fig. 113$_{10}$ (Fig. 23c1; revision).

1932 ***Gonostomum (Oxytricha) affine* (Stein, 1859)** – Kahl, Tierwelt Dtl., 25: 598, 115$_{1}$, not Fig. 113$_{9}$, 115$_{2–4}$ (redrawing of *G. andoi* [Fig. 23b]; see remarks).

1950 ***Gonostomum strenuum* (Engelmann)** – Kudo, Protozoology, p. 670, Fig. 314i (redrawing of Fig. 23a; textbook on protozoology).

1972 ***Gonostomum strenuum* (Engelmann, 1862) Sterki, 1878** – Borror, J. Protozool., 19: 14, Fig. 42 (Fig. 23c2, a schematised redrawing of Kahl's redrawing [Fig. 23c1] of Fig. 23a; revision of hypotrichs).

1974 ***Gonostomum strenuum* Engelmann** – Stiller, Fauna Hung., 115: 89, 54. ábra A (redrawing of Fig. 23a; guide to Hungarian hypotrichs).

1984 ***Gonostomum strenua* (Engelmann, 1862) Sterki, 1878** – Maeda & Carey, Bull. Br. Mus. nat. Hist., 47: 11, Fig. 4 (redrawing of Fig. 23a; detailed revision of *Gonostomum* and *Trachelostyla*).

1990 ***Gonostomum strenua* (Engelmann, 1862)** – Song, J. Protozool., 37: 249, Fig. 1–21, Tables 1, 2 (Fig. 23d; Fig. 122a–u in Berger 1999; detailed description of Chinese population and analysis of cell division; voucher slides are likely deposited in the Ocean University of Qingdao, China).

1997 ***Gonostomum strenua*** – Olmo & Téllez, Quekett J. Microscopy, 38: 4, Fig. 2 (micrograph of a late divider).

1997 ***Gonostomum strenua* Engelmann, 1862** – Olmo & Téllez, Arch. Protistenk., 148, Fig. 1–16, Table 1 (Fig. 23e, f; description of morphology and cell division of Spanish population).

1998 ***Gonostomum strenua* Engelmann, 1862** – Olmo Rísquez, Dissertation, p. 45, Fig. 1–16, Tabla 1 (Fig. 23e, f; description of morphology and morphogenesis of Spanish population [already published by Olmo & Téllez 1997]).

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[1] Engelmann (1862) provided the following diagnosis: Körper metabolisch, lanzettlich, nach vorn stärker, nach hinten schwächer verschmälert. Die adorale Wimperreihe längs des linken Seitenrandes hinziehend, und plötzlich knieförmig nach innen gebogen. Kein deutliches Peristomfeld. Zehn griffelförmige Wimpern auf dem Stirnfeld, zwei schräge Reihen borstenförmiger Wimpern, deren eine sich bis auf die hintere Körperhälfte fortsetzt. Vier Afterwimpern. Zwei borstenförmige Endwimpern.

1998 ***Amphisiella strenua* nov. comb.** – Olmo Rísquez, Dissertation, p. 53 (combination with *Amphisiella*; see remarks).

1999 ***Gonostomum strenuum* (Engelmann, 1862) Sterki, 1878** – Berger, Monographiae biol., 78: 384, Fig. 121, 122a–u, Tables 3, 23 (detailed review).

2000 ***Gonostomum affine* (Stein, 1859) Sterki, 1878** – Foissner, Stud. Neotrop. Fauna & Environm., 35: 72, Fig. 84, 85, Table 4 (Fig. 23g, h; misidentification; description of a Venezuelan population; one voucher slide is deposited in the Upper Austrian Museum in Linz).

2001 ***Gonostomum strenuum* (Engelmann, 1862) Sterki, 1878** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 64 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2001 ***Gonostomum strenuum* (Engelmann, 1862) Sterki, 1878** – Foissner, Stoeck, Schmidt & Berger, Acta Protozool., 40: 93, Fig. 6, 14, Table 1 (Fig. 23k; description of Australian population and comparison with *G. affine* using morphology and RAPD-fingerprinting).

2001 ***Gonostomum strenuum* (Engelmann, 1862)** – Bernhard, Stechmann, Foissner, Ammermann, Hehn & Schlegel, Molecular Phylogenetics and Evolution, 21: 87 (estimation of phylogenetic position using SSUrRNA; EMBL Accession No. AJ310493).

2002 ***Gonostomum strenuum* (Engelmann, 1862) Sterki, 1878**[1] – Foissner, Agatha & Berger, Denisia, 5: 815, Fig. 177a–d, Table 157 (Fig. 23i, j; description of Namibian population and neotypification).

Nomenclature: No derivation of the name is given in the original description or any other paper, including my review (Berger 1999). The species-group name *strenu·us, -a, -um* (Latin adjective [m; f; n]; brisk, prompt, active, vigorous, strenuous; Brown 1954, p. 762) is likely an allusion to the movement, which is somewhat more rapid than that of *G. affine*. The name *andoi* is likely a dedication to a person with the family name Ando. For details on the somewhat cryptic combination with *Gonostomum* by Sterki (1878), see Berger (1999, p. 384). For neotypification, see the remarks section below. *Gonostomum strenuata* in Song (1990, p. 256) is an incorrect subsequent spelling (several further incorrect subsequent spellings are reviewed by Berger 1999). Note that the "*Gonostomum strenua* Engelmann, 1862" in the heading of Olmo & Téllez (1997) is incorrect, because the basionym is *Oxytricha strenua* Engelmann, 1862. "*Oxytricha strenuum* Engelmann, 1862" in Jankowski (1979, p. 55) is the incorrect combination of the feminine genus-group name *Oxytricha* and the neuter species-group name *strenuum*.

Oxytricha strenua is the type species of *Plagiotricha* Kent, 1882 by original designation. Borror (1972) incorrectly assumed that it is the type species of *Gonostomum* by monotypy, a mistake which was taken over by Jankowski (1979, p. 55). For detailed explanation of this issue, see nomenclature at genus section.

Remarks: The list above contains all synonyms. *Gonostomum strenuum* is now a well defined species although the separation from the type species, *G. affine*, can be

[1] Foissner et al. (2002a) provided the following diagnosis (see remarks): Size 80–130 × 25–55 µm in vivo; ellipsoidal. 2 macronuclear nodules. Cortical granules colourless or yellowish, 1.0–1.5 × 0.6 µm in size, form distinct fringe. On average 20–27 right marginal, 15–17 left marginal, 4–5 frontoterminal, 10–12 frontoventral, and 4–5 pretransverse and transverse cirri; 1 buccal cirrus right of anterior half of paroral; frontoventral cirral row V composed of 5–9 cirri, that is, long and surpassing buccal vertex. Adoral zone about 50% of body length, composed of 28–29 membranelles on average. Usually 10–13 paroral cilia.

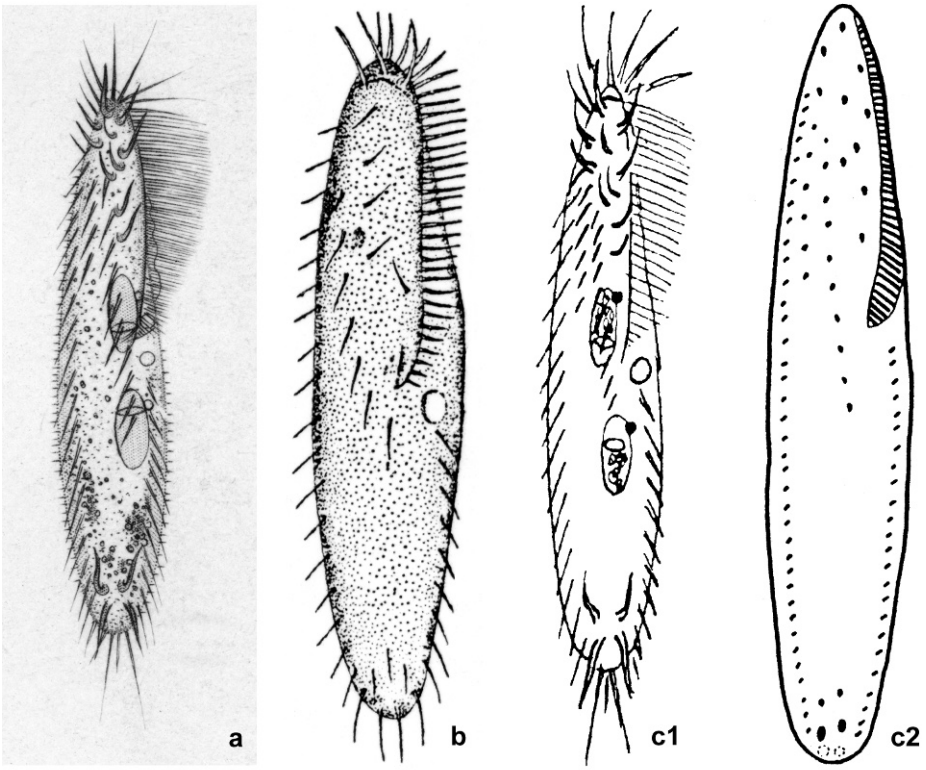

Fig. 23a–c *Gonostomum strenuum* (a, from Engelmann 1862; b, from Shibuya 1929; c1, after Engelmann 1862 from Kahl 1932; c2, after Kahl 1932 [after Engelmann 1862] from Borror 1972. From life). **a, c1, c2:** Ventral view showing cirral pattern and nuclear apparatus, about 150 µm. A very important feature of *G. strenuum* is the frontoventral row which extends onto the postoral area; this is rather easily recognisable even in life. By contrast, another very important characteristics, the increased number of frontoterminal cirri (see Table 14) is unequivocally recognisable only after protargol impregnation. Note that Borror's illustration is a modified redrawing of Kahl's figure, which itself is a redrawing of Stein's original illustration. **b:** Ventral view of the junior synonym *G. andoi*, about 100 µm. Page 146.

a problem occasionally. Thus, protargol impregnation is recommended to check the cirral pattern (see below).

Gonostomum andoi Shibuya, 1929 was synonymised with *G. affine* by Kahl (1932, p. 598), a proposal followed by Borror (1972, p. 14) and Buitkamp (1977, p. 125). I preliminary accepted this decision in the first volume of the monograph, but already discussed that it cannot be excluded that it is identical with *G. strenuum* because the frontoventral cirral row terminates clearly behind the level of the buccal vertex (Berger 1999, p. 370, 384). In addition, I discussed that *G. affine* sensu Goodey (1911) could be a misidentification for the same reason. Now distinctly more is known about the differences between *G. strenuum* and *G. affine* and therefore I classify *G. andoi* (Fig. 23b) and *G. affine* sensu Goodey (1911; Fig. 118o in

Berger 1999) as synonyms of *G. strenuum*. Of course we will never know what they really are because permanent preparations are not available.

Hemberger (1982, p. 190) synonymised *Gonostomum strenuum* with the type species, although after some hesitation, mainly because the species was not redescribed for more than 100 years and *G. affine* sometimes also has a rather high number of frontoventral cirri.

Since no specimens from the type population (Engelmann 1862) are preserved, Foissner et al. (2002a) fixed a "characteristic" population from Namibia as neotype to define the species objectively. The Namibian specimens (Fig. 23i, j, Table 14) are highly similar to the populations described by Engelmann (1862; Fig. 23a) from Germany, by Song (1990, Fig. 23d; Fig. 122a–u in Berger 1999) from China, by Olmo & Téllez (1997; Fig. 23e, f) from Spain, and by Foissner et al. (2001; Fig. 23k) from Australia. Thus, all these populations were used for the improved diagnosis given by Foissner et al. (2002a; see footnote 1 on p. 147), and only some supplementary data from the neotype population have been provided. Accordingly, *Gonostomum strenuum* can be clearly separated from the type species (*G. affine*) by the following combination of features (Foissner et al. 2002a):

(i) 3–6, usually four frontoterminal cirri against usually two, a feature already recognised and illustrated by Engelmann (1862, Fig. 23a). Likely the increased number in *G. strenuum* is an apomorphy because two frontoterminal cirri correspond the supposed ground pattern of the hypotrichs (Berger 2008, p. 26).

(ii) The frontoventral row originating from anlage V is composed of 5–9 cirri and therefore usually ends behind the level of the buccal vertex against short and terminating ahead of level of buccal vertex because made up of only two cirri. In *G. affine* these two cirri are homologous to the postoral ventral cirri V/3 and V/4 of the 18-cirri hypotrichs (Fig. 3a), indicating that the increased number in *G. strenuum* is the derived state.

(iii) In total, *Gonostomum strenuum* has 20–25 frontoventral cirri[1] whereas *G. affine* has only 6–15, on average 11 frontoventral cirri (data from 18 soil populations compiled by Foissner 2000 and Foissner et al. 2001). An 18-cirri hypotrich has 13 (18 minus five transverse cirri) such cirri showing that *G. strenuum* has 7–12 cirri more than an 18-cirri hypotrich, whereas *G. affine* has, on average, two such cirri less than the last common ancestor of the hypotrichs. Interestingly, in both species the number of transverse cirri is usually distinctly reduced, namely from five in the ground pattern (Fig. 2a) to usually two (Fig. 23a, d, e, g, i, k).

(iv) *Gonostomum strenuum* has conspicuous cortical granules (Fig. 122b, c in Berger 1999), whereas these organelles are usually lacking or very indistinct in *G. affine* (Berger 1999, Foissner et al. 2002a).

(v) The left marginal row terminates at the midline of the cell in *G. strenuum* (Fig. 23d, e, g, i, k), that is, more or less distinctly behind the transverse cirri whereas the rearmost left marginal cirrus is usually at the level of the transverse cirri

[1] Frontal cirri, buccal cirrus, frontoventral cirri, frontoterminal cirri, "postoral" ventral cirri, and pretransverse ventral cirri included.

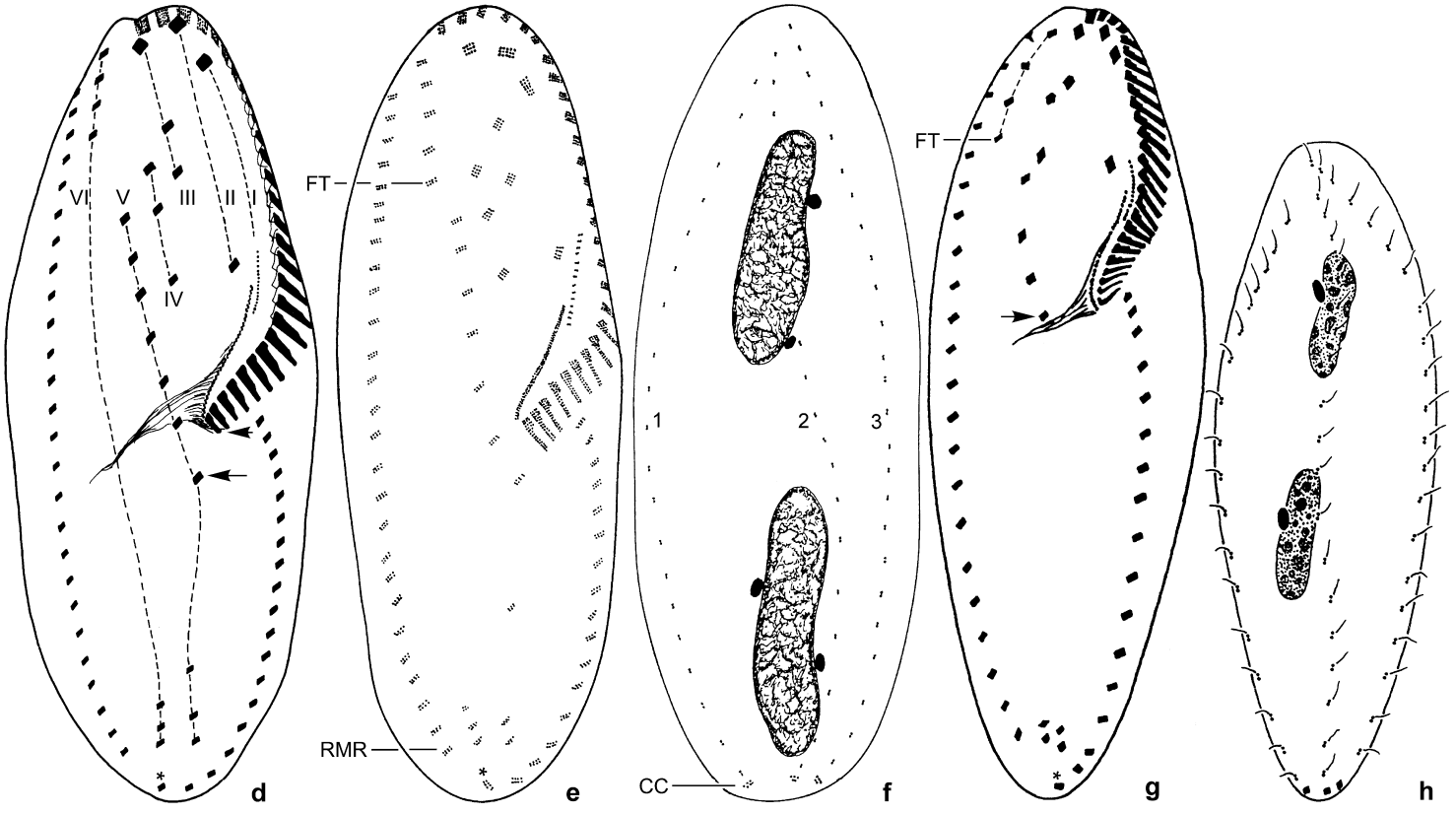

Fig. 23d–h *Gonostomum strenuum* (d, from Song 1990; e, f, from Olmo & Téllez 1997; g, h, from Foissner 2000. Protargol impregnation). Infraciliature of ventral (d, e, g) and dorsal (f, h) side. Note that in *G. strenuum* the left marginal row ends in cell midline (asterisks). **d:** Chinese population, 100 µm. Long arrow marks rear end of frontoventral row which (usually) terminates distinctly behind the level of the adoral zone (buccal vertex; short arrow). **e, f:** Spanish population, e = 123 µm, f =

Legend continued on p. 151

in *G. affine* (Fig. 3a, 12a–f, 14a, d; Fig. 117d, h, o, p, 120a in Berger 1999). Admittedly, this is a sophisticated, but obviously stable feature, which, however, should only be used in combination with the other features to assign a population either to *G. strenuum* or to *G. affine*.

Foissner et al. (2001) studied the biogeographical differences in *G. affine* from Austria, Saudi Arabia, Namibia, Venezuela, and Brazil using morphological features and RAPD-fingerprint analysis. In addition, an Australian population of *G. strenuum* was included in the study (Fig. 23k). The morphological analysis based on the coefficient of racial likeness demonstrated a very clear separation of *G. strenuum* from *G. affine* (Fig. 13a). By contrast, a RAPD-fingerprint tree with the association (band sharing) index of Simpson yielded a very close relationship of *G. strenuum* and the Namibian populations of *G. affine*, indicating that this method alone is insufficient for taxonomic analyses.

Olmo Rísquez (1998, dissertation) transferred the present species to *Amphisiella* Gourret & Roeser, 1888, a combination overlooked by Berger (2001, 2008). At superficial consideration, such a combination looks plausible because the 3–6 frontoterminal cirri and the cirri originating from anlage V produce indeed a more or less distinct "amphisiellid" median cirral row, which, however, shows a distinct break where the two portions join up (Fig. 23e). The oral apparatus, however, clearly shows that *G. strenuum* does not belong to the amphisiellids because members of this group lack the gonostomatid adoral zone and the short undulating membranes (Berger 2008). A classification of *G. strenuum* in *Amphisiella* would make this marine genus inhomogeneous because true *Amphisiella* species lack caudal cirri and have more than three dorsal kineties whereas *Gonostomum* has three kineties, each bearing a caudal cirrus, a combination corresponding the ground pattern of hypotrichs (Berger 2008). The dissertation by Olmo Rísquez (1998) contains an illustration of a live specimen not shown in present book.

Foissner (2000) characterised a *G. affine* population from Venezuela (Fig. 23g, h, 24b–e, Table 14). The frontoventral row extends to the buccal vertex or even onto the postoral area. Thus, he was uncertain about the identification, supposed that the Venezuelan population is in between *G. affine* and *G. strenuum*, and even questioned the validity of *G. strenuum*. Finally he suggested that gene sequence data are needed to estimate the status of this population from *Espeletia* leaves. Somewhat later, we stated that this population is more closely related to *G. strenuum* than to the *G. affine*-group (Foissner et al. 2002a, p. 817), and in the present book I consider it as synonym of *G. strenuum*, because the classification in *G. affine* makes the characterisations of both species rather imprecise.

← 119 µm. **g, h:** Venezuelan specimen, 98 µm. The frontoventral row of this population does not extend clearly onto the postoral area (arrow) as in other populations; nevertheless I suppose that it is *G. strenuum* because of the increased number of frontoterminal cirri. Note that the left frontal cirrus is not increased in this population (Foissner 2000, figure legend). CC = caudal cirri, FT = frontoterminal cirri, RMR = rear end of right marginal row, I–VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 146.

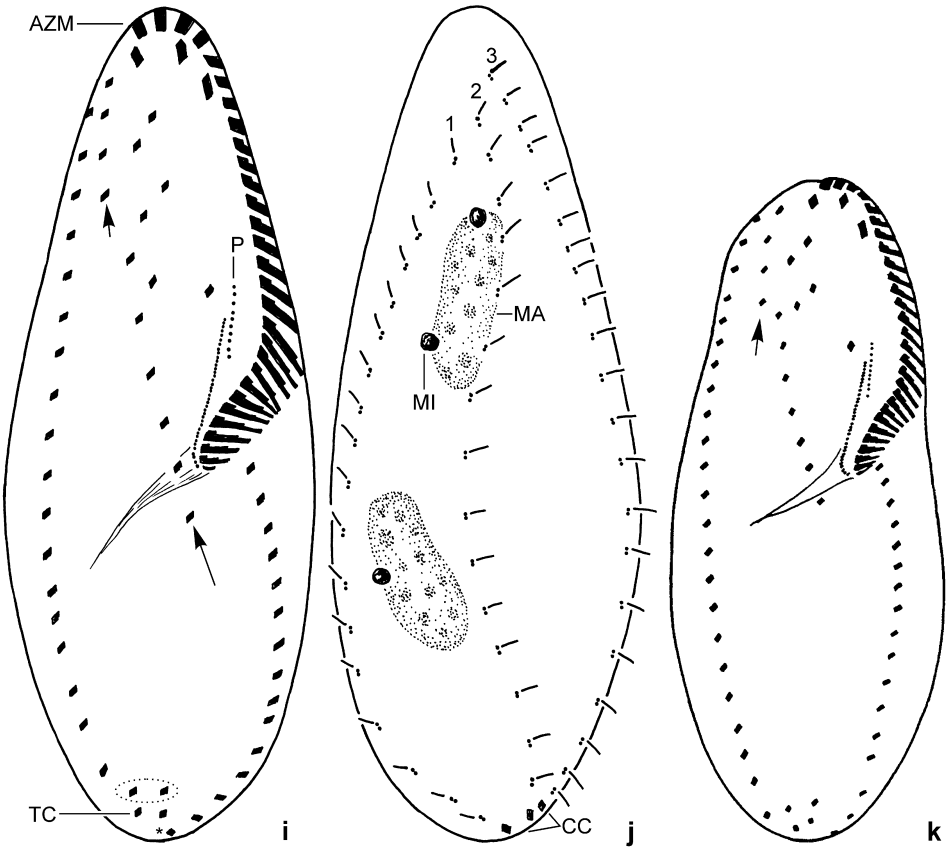

Fig. 23i–k *Gonostomum strenuum* (i, j, from Foissner et al. 2002a; k, from Foissner et al. 2001. Protargol impregnation). **i, j:** Infraciliature of ventral and dorsal side and nuclear apparatus of neotype specimen from Namibia, 76 µm. Long arrow marks rear end of frontoventral row, short arrow denotes row formed by frontoterminal cirri. Pretransverse ventral cirri encircled. **k:** Infraciliature of ventral side of specimen from Australia, 93 µm. Arrow marks frontoterminal cirri. Note that perhaps the rearmost left marginal cirrus is not shown/illustrated because it is exactly at the margin of the cell. AZM = distal end of adoral zone of membranelles, CC = caudal cirri, MA = macronuclear nodule, MI = micronucleus, P = paroral, TC = transverse cirri, 1–3 = dorsal kineties. Page 146.

Borror (1972, p. 14) put *Oxytricha tricornis* Milne, 1886 into the synonymy of *G. strenuum*. However, this is a not very well described marine species (Irish Sea?) with very prominent frontal adoral membranelles, indicating that the synonymy is incorrect. For review of this species, see Berger (1999, p. 241).

Gonostomum strenuum sensu Lundin & West (1963; Fig. 117u in Berger 1999) is a *G. affine*. For two insufficiently described populations, see Berger (1999, p. 384, 395, Fig. 232p, 241e). Çapar (2007) described a Turkish population after live observation and protargol impregnation. The cirral pattern does not show the *strenuum*-aspect, that is, the postorally extending frontoventral row and the increased number

of frontoterminal cirri, which are not shown (lacking? overlooked? misinterpreted?) in the illustration (Fig. 29a, b). Because of these deficiencies, the Turkish population is classified as insufficient redescription treated at the end of the *Gonostomum* chapter (p. 171).

Morphology: For a detailed description of the morphology, see Berger (1999, p. 384). The present chapter therefore contains only additional observations from the neotype population from Namibian site (49) (Fig. 23i, j, Table 14), some observations from other populations, and a review of the new synonym *G. andoi* (Fig. 23b). The morphometries of all populations studied so far are compiled in Table 14.

Body size of neotype specimens about 80–110 × 25–35 µm in life. Body flattened about 2:1 dorsoventrally. Contractile vacuole with longitudinal collecting canals. Cortical granules in loose rows, form distinct fringe; individual granules ellipsoidal, about 1.0–1.2 × 0.6 µm, yellowish, compact and thus bright, stain red with methyl green-pyronin, but are not ejected and do not impregnate with the protargol method used. Cytoplasm colourless, posterior cell portion usually with many bright lipid droplets 2–3 µm across. Glides rather rapidly on microscope slide. Adoral zone extends over 51% of body length on average, bases of largest membranelles about 5 µm wide in life. Paroral cilia about 6 µm long in life. Frontoventral, marginal, and caudal cirri about 15 µm long in life, transverse cirri about 20 µm, and dorsal bristles about 3 µm. Dorsal kineties become slightly shorter anteriorly from right (kinety 3) to left (1; Fig. 23j); a feature also known from the Spanish and the Venezuelan population (Fig. 23f, h), but not from the Chinese (Fig. 122e in Berger 1999).

Details on infraciliature, oral apparatus, and dorsal ciliature of populations described by Foissner (2000) and Foissner et al. (2001), see Fig. 24a–e.

The Spanish population studied by Olmo & Téllez (1997) agrees very well with the other populations, so that only some interesting details are briefly reviewed. Cortical granules stain in silver-carbonate preparations (Fig. 3 in Olmo & Téllez 1997); when ejected they become about 6 µm long and spindle-shaped. Usually moderately rapid creeping, sometimes rotating about main body axis. All adoral membranelles composed of four kineties, namely two short with 3–5 basal bodies each and two long kineties with 14–16 basal bodies each (Fig. 23e). Dorsal kineties composed of 14–25 basal body pairs (Fig. 23f). Cyst spherical with smooth cyst wall, about 40 µm across (Fig. 4 in Olmo & Téllez 1997).

Gonostomum andoi Shibuya, 1929 (Fig. 23b): Body size about 100 × 25 µm. Body very flexible, elongate elliptical, left margin more convex than right; both ends rounded; dorsoventrally flattened. Two ovoid macronuclear nodules, difficult to recognise in life; position neither described nor illustrated; likely in central portion of cell. Contractile vacuole almost spherical, slightly behind buccal vertex near left cell margin. Micronuclei, presence/absence of cortical granules, details of cytoplasm, and movement not described. Adoral zone gonostomatid, occupies about 50% of body length; specimen illustrated with 33 membranelles (value must not be overinterpreted because from live-observation). “Undulating membrane” (likely he meant the paroral) inconspicuous, appears to be confined to rear end of oral apparatus.

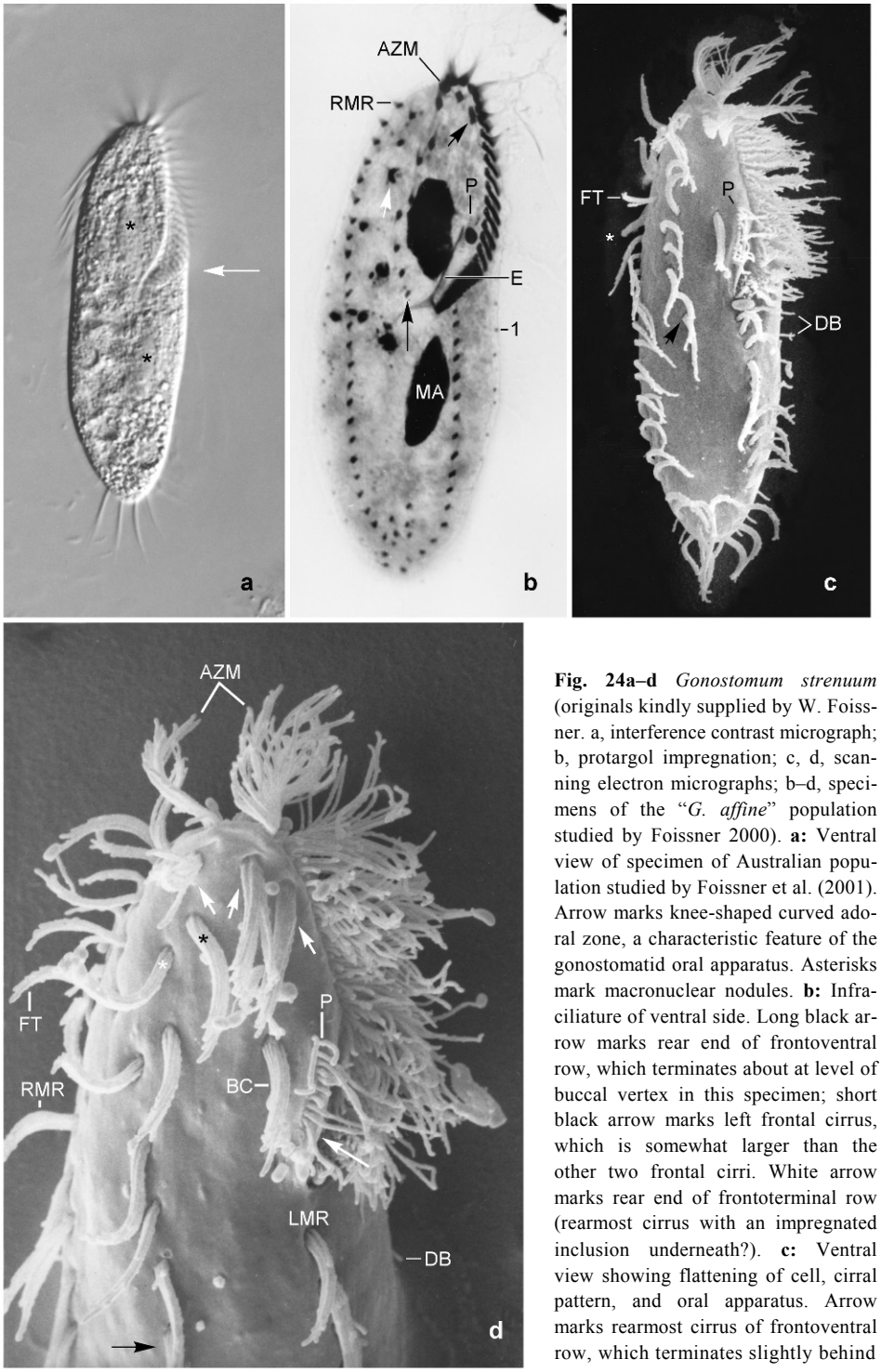

Fig. 24a–d *Gonostomum strenuum* (originals kindly supplied by W. Foissner. a, interference contrast micrograph; b, protargol impregnation; c, d, scanning electron micrographs; b–d, specimens of the "*G. affine*" population studied by Foissner 2000). **a:** Ventral view of specimen of Australian population studied by Foissner et al. (2001). Arrow marks knee-shaped curved adoral zone, a characteristic feature of the gonostomatid oral apparatus. Asterisks mark macronuclear nodules. **b:** Infraciliature of ventral side. Long black arrow marks rear end of frontoventral row, which terminates about at level of buccal vertex in this specimen; short black arrow marks left frontal cirrus, which is somewhat larger than the other two frontal cirri. White arrow marks rear end of frontoterminal row (rearmost cirrus with an impregnated inclusion underneath?). **c:** Ventral view showing flattening of cell, cirral pattern, and oral apparatus. Arrow marks rearmost cirrus of frontoventral row, which terminates slightly behind

According to Shibuya (1929), eight frontal cirri and seven ventral cirri present; these 15 cirri can be assigned as follows: three enlarged frontal cirri; one buccal cirrus somewhat ahead of proximal end of adoral zone; four frontoventral cirri form row about in midline; seven frontoventral cirri (likely including two or more frontoterminal cirri) form an oblique row extending from near right body margin at 18% of body length to cell midline at about 55% of body length, that is, row ending more or less distinctly behind rear end of adoral zone. Three transverse (= "anal") cirri form triangular pattern (likely one pretransverse ventral cirrus included). Right marginal row (about 20 cirri illustrated; value must not be overinterpreted) slightly shortened anteriorly, posteriorly not separated from left marginal row (ca. 11 cirri), which begins at level of contractile vacuole; I suppose that the gap between the marginal rows is occupied by the caudal cirri, which are, however, not mentioned in the original description. Dorsal infraciliature (number and arrangement of dorsal kineties, length of bristles; presence/absence of caudal cirri) not described.

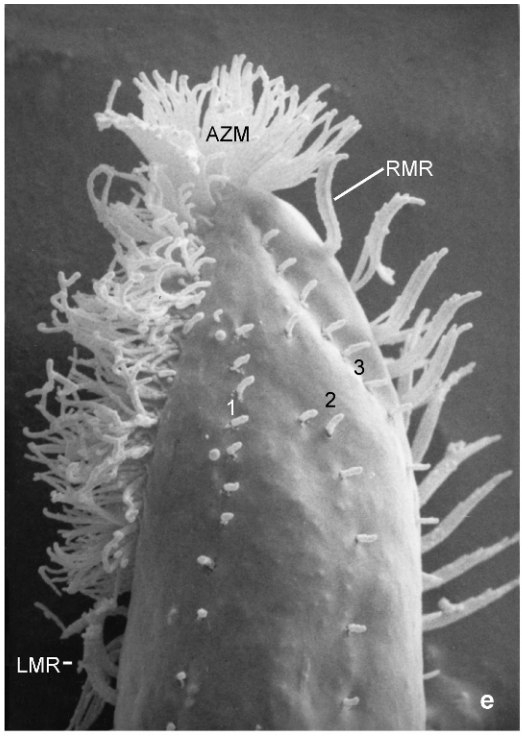

Fig. 24e *Gonostomum strenuum* (original kindly supplied by W. Foissner. Scanning electron micrograph; specimens of the "*G. affine*" population studied by Foissner 2000). Ciliature of dorsal side of anterior body half. Note that bacteria and/or extruded cortical granules may feign dorsal bristles in scanning electron micrographs. Anterior end of kinety 2 not quite normal in this specimen. AZM = adoral zone of membranelles, LMR = left marginal row, RMR = right marginal row, 1–3 = dorsal kineties. Page 146.

Molecular data: The SSU rDNA of *Gonostomum strenuum* (Australian population studied by Foissner et al. 2001; Fig. 13a, 23k, Table 14) is, like that of *G. na-*

← level of buccal vertex. Asterisk marks right marginal cirrus. **d:** Ventral view of anterior body half. Short white arrows mark frontal cirri, long white arrow denotes (inner; left) margin of buccal lip; black arrow marks (end of?) frontoventral row. Asterisk denotes parabuccal cirrus (III/2). AZM = adoral zone of membranelles, BC = buccal cirrus, DB = dorsal bristles, E = endoral, FT = rearmost frontoterminal cirrus (note that in [d] this is not the cirrus whose base is marked with a white asterisk!), LMR = left marginal row, MA = macronuclear nodule, P = paroral, RMR = right marginal row, 1 = dorsal kinety 1. Page 146.

mibiense, 1773 base-pairs long (EMBL Accession No. AJ310493). The two trees provided by Bernhard et al. (2001) include only three non-stylonychid hypotrichs, namely, *Gonostomum strenuum*, the oxytrichid *Oxytricha granulifera* (for review, see Berger 1999, p. 197), and the urostyloid *Anteholosticha multistilata* (for review, see Berger 2006a, p. 405), and *Halteria grandinella*, an oligotrich-like perilemmaphorid of uncertain position (Foissner et al. 2004; for review, see Foissner et al. 1999, p. 559). Thus, the trees are rather vague, but show two noteworthy results: (i) *Gonostomum strenuum* is a non-stylonychid hypotrich; and (ii) *Gonostomum strenuum* branches off at the same level or even earlier than the sole urostyloid included, indicating that it is not an oxytrichid as supposed by Berger & Foissner (1997) and Berger (1999). A basal branching of *G. strenuum* was also noticed by Agatha et al. (2004, 2005), Agatha & Strüder-Kypke (2007), Affa'a et al. (2004), Kim et al. (2005), Gong et al. (2007; only *Protogastrostyla pulchra* branches off earlier in the hypotrichs), Miao et al. (2007, 2009a), Schmidt et al. (2007), Sonntag et al. (2008; *Trachelostyla pediculiformis* is more closely related to the oligotrichs than to the hypotrichs), Tsai et al. (2008), Paiva et al. (2009), Hu et al. (2009b; only their Fig. 3; in their Fig. 2 *Gonostomum* is the sistergroup of the oxytrichids), and Kim et al. (2010). By contrast, Modeo et al. (2003) provided two trees invariably showing an sistergroup relationship with the taxon *Paraurostyla weissei* + stylonychines. According to the tree published by Foissner et al. (2004), *Gonostomum strenuum* is closely related to *G. namibiense* and *Orthoamphisiella breviseries* and forms a rather distinct cluster together with *Engelmanniella*, *Hemiurosoma*, *Halteria*, *Oxytricha*, *Onychodromopsis*, and the uroleptids. The urostyloids are the most basal branch in this tree. A similar position was estimated by Gong et al. (2006), Shao et al. (2007), and Li et al. (2008); in the former two papers with *Trachelostyla pediculiformis* (for review, see Berger 2008, p. 478) as closely related species to the *Gonostomum-Orthoamphisiella* group. In the tree published by Li et al. (2009), *Gonostomum strenuum* is in the same cluster as just described, but *Trachelostyla* and *Amphisiella* form the basal branch of the hypotrichs. The analysis provided by Foissner & Stoeck (2008) is similar to that by Foissner et al. (2004), but the uroleptids are not so closely related. By contrast, *Gonostomum namibiense* and *G. strenuum* are distinctly separated from *Orthoamphisiella breviseries* in further analyses (Foissner & Stoeck 2006a, 2008). In the trees published by Richards et al. (2005), Kim et al. (2007), Doherty et al. (2007), and Miao et al. (2009), the number of hypotrichs included is obviously too small to provide reliable results. In a tree published by Kim et al. (2007) with almost 70 species from all major groups of ciliates, *Gonostomum strenuum* is more closely related to the oligotrichs than to *Amphisiella magnigranulosa* (for review, see *Uroleptoides magnigranulosus* in Berger 2008, p. 273), indicating that this analysis is incorrect at least in this respect.

All these analyses show that details in molecular trees should not be overinterpreted. However, there is a general trend to a basal branching of *Gonostomum* within the hypotrichs, a position which is in agreement with the new interpretation of the morphological data, namely, (i) that the 18-cirri pattern is not a novelty of the oxy-

trichids, as supposed by Berger & Foissner (1997) and Berger (1999), but of the hypotrichs (Berger 2006, p. 33; 2008, p. 23; 2008a), and (ii) that the simple dorsal kinety pattern (lack of dorsomarginal kineties and oxytrichid kinety fragmentation) is an old feature within the hypotrichs, and not a novelty of *Gonostomum*, as supposed by Berger (1999). Thus, *Gonostomum*, respectively, the Gonostomatidae are very likely non-dorsomarginalian hypotrichs.

Occurrence and ecology: *Gonostomum strenuum* is – like *G. affine* – obviously a cosmopolitan species occurring both in limnetic and terrestrial habitats; however, it is much rarer than the type species. The original type locality is a small ditch in Leutzsch, a village in the western environs of Leipzig, Germany, where Engelmann (1862) found it between *Lemna* sp.

Due to the neotypification, the new type locality of *Gonostomum strenuum* is in Namibia, namely on the area of the Bambatsi Guest Farm (1150 m above sea-level; 20°10'S 15°25'E) between the towns of Khorixas and Outjo (Foissner et al. 2002a). It occurred in a sample (collected on 27.12.1999) composed of dark grey mud and 0–2 cm soil layer containing grass roots and the orange and green algae cover from dry and wet puddles of roads within the farm area. For further details, see Foissner et al. (2002a, p. 25; site 49). Unfortunately, the new type locality was destroyed one year later because the roads have been upgraded (Foissner et al. 2002a, p. 25). The Australian population studied by Foissner et al. (2001) is from a soil sample of the River Murray floodplain near Albury (37°S 147°E).

Further records of *G. strenuum* substantiated by morphological data: upper soil layer in Baguan hill (ca. 50 m sea-level) in Qingdao, China (Song 1990); moss samples from emergent (likely non-flooded) stones at the bank of the River Guadarrama (1188 m sea-level), Central Spain (Olmo & Téllez 1997); decaying *Espeletia* leaves (pH 6.0) from dead, rotting trunks, very likely 100–150 years old from the Páramo de Piedras Blaces (08°52'N 70°48'W) at 4200 m sea-level, Cordillera de Mérida, Venezuela, about 2 km east of the Pico del Aquila (Foissner 2000; as *G. affine*; see remarks).

Records published after the review by Berger (1999) appeared (for pre-1999 records, see Berger 1999, p. 391): up to 2 ind. ml^{-1} in streamlets in the spring area below the Velky Javorník near Bratislava, Slovakia (Tirjaková 1997, p. 15; Tirjaková & Stloukal 2004, p. 16; further record from Slovakia: Tirjaková 2005, p. 21); Thailand (Charubhun & Charubhun 2000, p. 491); soil from a constructed mangrove wetland in the Futian Nature Reserve of Shenzhen, South China (Chen et al. 2009, p. 716).

The type locality of *Gonostomum andoi* is soil from the experimental farm at Nishigahara near Tokyo, Japan. Perhaps Shibuya (1929) cultured it in 2% timothy-hay infusion. No further records of synonym published.

The specimens of the neotype population feed – like those of the other populations (for review, see Berger 1999) – on bacteria (Foissner et al. 2002a).

Gonostomum gonostomoidum (Hemberger, 1985) Berger, 1999
(Fig. 25a–j, Table 14)

1982 ***Trachelochaeta gonostomoida* n. spec.**[1] – Hemberger, Dissertation, p. 45, Abb. 6a–e (Fig. 25a, b; Fig. 124a–f in Berger 1999; see nomenclature).

1985 ***Trachelochaeta gonostomoida* n. spec.**[2] – Hemberger, Arch. Protistenk., 130: 400, Abb. 3 (Fig. 25a, b; original description; no formal diagnosis provided; type slides are deposited in the Institut für Landwirtschaftliche Zoologie und Bienenkunde, University of Bonn, Germany).

1999 ***Gonostomum gonostomoida* (Hemberger, 1985) comb. nov.** – Berger, Monographiae biol., 78: 392, Fig. 124a–f, Table 23 (combination with *Gonostomum* and detailed review).

2001 ***Gonostomum gonostomoida* (Hemberger, 1985) Berger, 1999** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 89 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2006 ***Gonostomum gonostomoida* (Hemberger, 1985)** – Kim & Shin, Korean J. syst. Zool., 22: 210, Fig. 3A–E, 4A–F, Tables 1–3 (Fig. 25f–j; description of Korean population).

2008 ***Gonostomum gonostomoida*** – Kamra, Kumar & Sapra, Indian J. Microbiol., 48: 382, Fig. 6a–c, 8, 13a–d (Fig. 25c–e; description of Indian population).

Nomenclature: No derivation of the name is given in the original description and the review by Berger (1999). The species-group name *gonostomoida* is a composite of the genus-group name *Gonostomum* (see genus section for derivation) and the suffix *-id·us, -a, -um* ([m; f; n]; resembling, similar), obviously referring to the similarity with *Gonostomum* (note that Hemberger 1985 established this species in *Trachelochaeta*!). *Trachelochaeta* is feminine (see p. 300), *Gonostomum* is neuter (see above); thus, the ending of the species-group name has to be emended to *Gonostomum gonostomoidum* nom. corr.

Remarks: Hemberger (1982, 1985) was uncertain about the classification of this species because it differs from *G. affine* only by the presence of the long frontoventral row. However, since the morphogenesis of the present species and *G. affine* is different due to this long frontoventral row, he did not put this population into the synonymy of the rather variable *G. affine*. Hemberger made no comment why he assigned this species to *Trachelochaeta* with *T. bryophila* as type species (Fig. 56a, b). Likely he considered the long frontoventral row as essential agreement between *T. bryophila* and his population. By contrast, I transferred it to *Gonostomum* because of the high resemblance in the general habitus, the oral apparatus, and the cirral pattern

[1] This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3). See next footnote.

[2] According to the ICZN (1964), dissertations are not explicitly mentioned under Article 9, which describes all those acts that do not constitute a publication within the meaning of the Code. Thus, Hemberger's (1982) thesis, for which the ICZN (1964) has to be applied, could possibly also be considered as original description of the present species and many other taxa first described in this paper. Unfortunately, the situation is rather complicated and almost each thesis would need a detailed analysis whether or not it meets the requirements of publication (P. Tubbs, ICZN, Natural History Museum, London, pers. comm.). Thus, I do not accept Hemberger (1982), but Hemberger (1985) as original description of all the taxa discovered by him. However, I include the thesis in the list of synonyms because it is one of the most important papers on hypotrichs since Kahl (1932). To avoid nomenclatural problems each new name mentioned by Hemberger (1982) is individually disclaimed for nomenclatural purposes (see corresponding footnotes).

(Berger 1999). I argued that the continuous frontoventral row of *G. gonostomoidum* (Fig. 25a) is homologous with the "indistinct", discontinuous row formed by the cirri of anlage VI in *G. affine* (Fig. 3a). In addition, the undulating membranes agree perfectly in *G. gonostomoidum* and *G. affine*, whereas nothing is known about these structures in *Trachelochaeta bryophila* (Fig. 56a). *Gonostomum* is basically a terrestrial group (limnetic records under edaphic influence are, however, known), whereas *T. bryophila* is a limnetic species. This is a further hint that Hemberger's assignment is not appropriate.

Gonostomum terrestre closely resembles the present species so that a detailed comparison is necessary. Unfortunately, *G. terrestre* is not described very detailed making such a proposal rather difficult. According to the illustration provided it has only five frontal-ventral-transverse cirri anlagen (Fig. 26a), whereas *Gonostomum gonostomoidum* has six anlagen, including the long frontoventral row (Fig. 25a). Such a difference is usually abundant enough to separate species. However, since one cannot exclude that the cirral pattern was not quite correctly recognised by Alekperov or misinterpreted by myself[1], the comparison is confined to the remaining frontoventral cirri (frontal cirri and buccal cirrus not included). According to Fig. 26a, *Gonostomum terrestre* has nine cirri whereas *G. gonostomoidum* has usually only five cirri (Fig. 25a, c), sometimes up to seven (Fig. 25h, i). Since this difference is also rather distinct, I (preliminary) do not synonymise *G. gonostomoidum* and *G. terrestre*. Regrettably, the morphometric data of both original descriptions have to be used with caution. *Gonostomum gonostomoidum* is 110–200 µm long according to Hemberger (1982, 1985; method [from life or after protargol impregnation] not clearly indicated), but has only about 33 membranelles, whereas *G. terrestris* – which is only 30–45 µm long – has about 45–50 membranelles. Interestingly, the number of left marginal cirri is about the same in both species (15 in Fig. 25a; 12 in Fig. 26a). These conflicting data indicate that they are not quite correct. Very certainly, the number of membranelles is distinctly overestimated in *G. terrestre*[2] and the size mentioned (30–45 µm) probably does not reflect the exact live data. By contrast, the body size in *G. gonostomoidum* is likely more or less distinctly overestimated. According to Fig. 25a, the distance between the individual basal bodies of the paroral is about 1.5 µm (note that the bar in the original description is 20 µm long; Hemberger 1985, p. 398). By contrast, this distance is about 0.5 µm in the Indian population (average body length 78 µm after protargol impregnation) of *G. gonostomoidum* (Kamra et al. 2008, Table 14) and 0.66 µm in the neotype population of *G. strenuum* (Table 14). In spite of the large value in the type population of *G. gonostomoidum*, its paroral looks like that of the other *Gonostomum* populations. Thus, I suppose that the scale bar and the measurements of *G. gonostomoidum* in Hemberger (1982, 1985) are incorrect, perhaps by a factor of two. Perhaps there is

[1] Perhaps row IV in Fig. 26a is actually formed from two anlagen? If so, then *Gonostomum terrestre* would have, like *G. gonostomoidum*, six frontal-ventral-transverse cirri anlagen.

[2] Unfortunately, the micrograph provided by Alekperov (2005; his Plate 22, Fig. 2) does not show the individual membranelles.

also a more or less distinct difference in the dorsal kinety pattern of the present species and *G. terrestre* (see there).

Gonostomum gonostomoidum has been redescribed two times recently. The two populations – one from Korea (Kim & Shin 2006; Fig. 25f–j) and the other from India (Kamra et al. 2008; Fig. 25c–e) – have basically the same cirral pattern as the type material (Hemberger 1985), but are smaller (60–121 µm in life, 85–124 µm in protargol preparations, Korean population; on average 78 µm in protargol preparations, Indian population) than the German population (110–200 µm, in life?). The distinctly lower values given in the redescriptions indicate that my suspicion about incorrect data in the original description discussed in the previous paragraph could be justified. There is second serious problem with *G. gonostomoidum*, namely, at present it is not known whether or not it has cortical granules. Hemberger (1982, 1985) did not check this feature because he studied mainly protargol-impregnated specimens where these organelles are usually not recognisable. In the text of the redescription, Kim & Shin (2006, p. 209, 210) mention that cortical granules are lacking. By contrast, in their Table 2 they write that such organelles are present, but they do not provide details. Kamra et al. (2008) confirm the cortical granules in *G. affine*, but make no comment about this feature in *G. gonostomoidum*. In addition, they neither discuss the redescription by Kim & Shin (2006) nor do they compare the present species with *Trachelochaeta terrestris* (Alekperov 2005).

All interphasic specimens illustrated so far have three more or less distinctly enlarged "transverse cirri" (Fig. 25a, c, g). Unfortunately, the exact origin and therefore the correct designation of these three cirri are not known. According to Hemberger (1982) one or two "terminal" cirri are formed at the end of the frontoventral row. Unfortunately, the only relevant divider illustrated shows only one enlarged cirrus both in the proter and the opisthe (Fig. 124f in Berger 1999). In addition, it is unclear from this illustration whether the enlarged transverse cirrus comes from anlage V or from anlage VI. Hemberger (1982) could not unequivocally recognise whether or not a transverse cirrus is formed from anlage V. In 1999 I discussed that the pattern shown could be explained by the preservation of parental transverse cirri (Berger 1999); however, this would result in a rather variable number of transverse cirri within a population because the proter would not gain parental cirri. Supposed that only two anlagen (V and VI) form transverse cirri, specimens with three enlarged cirri would have two transverse cirri (V/1, VI/1) and one pretransverse ventral cirrus (VI/2). Anyhow, more detailed ontogenetic data are needed to understand the pattern correctly. Interestingly, the same pattern is described for *G. terrestre* (Fig. 26a).

According to the phylogenetic analysis by Eigner (1997, p. 555; 1999, p. 46), the present species belongs to the Orthoamphisiellidae because a primordium is formed in the rightmost frontoventral row. Within the orthoamphisiellids it forms a subgroup with *Orthoamphisiella franzi* (= *Neowallackia franzi* in present book, p. 281), *O. stramenticola*, and *O. grelli* because the number of cirri in the two rightmost rows is in the range of 9–30. However, note that Eigner used only six features to estimate

the phylogenetic relationships of 41 species, resulting in a low discrimination. The anteriormost two cirri of the long frontoventral row (= row VI) are homologous to the frontoterminal cirri of the 18-cirri hypotrichs. Many ontogenetic data revealed that these two frontoterminal cirri do not participate in primordia formation (for review, see Berger 1999, 2006a, 2008). In *G. gonostomoidum* a long primordium (basically a primary primordium) is formed in the middle portion of row VI. As expected, the anteriormost two frontoterminal cirri are not involved in primordia formation.

The three populations described so far are characterised separately because of the problems discussed above. In addition, they have been found in rather distant areas (Germany, Korea, India) of Eurasia so that one cannot exclude that they turn out to be (already) subspecies due to allopatry. Perhaps the next species (*G. terrestre*) is also only a (small) subspecies of *G. gonostomoidum*.

Morphology: At first the type population described by Hemberger (1985) is characterised (Fig. 25a, b, Table 14). Body size (in life? after protargol impregnation?) 110–200 × 30–50 µm (for problems with this feature, see remarks); specimen illustrated about 180 × 65 µm (Fig. 25a). Body outline lanceolate, more or less as in *G. affine*. Macronuclear nodules ellipsoidal (length:width ratio about 1.6:1; Fig. 25b); position not mentioned; likely roughly in central body portion as in *G. affine*. Probably more or less invariably one micronucleus attached to each macronuclear nodule; individual micronuclei roughly globular to ellipsoidal (Fig. 25b). Contractile vacuole in ordinary position, that is, left of buccal vertex close to cell margin. Presence/absence of cortical granules, cytoplasmic inclusions, and movement not described. Oral apparatus as in *G. affine*. Paroral of specimen illustrated about 16 µm long and composed of 11 basal bodies/cilia (Fig. 25a), resulting in a distance of about 1.5 µm between the individual basal bodies (for problems with this value, see remarks). Endoral composed of narrowly spaced basal bodies, optically slightly overlapping anteriorly with paroral. Frontal cirri gonostomatid, that is, basis of leftmost cirrus slightly longer than that of the other two cirri and somewhat displaced posteriad. Buccal cirrus right of paroral. Specimen illustrated with typical "18-cirri pattern" in frontal area, except that not only two frontoterminal cirri (cirri VI/3, VI/4) are present, but a long row extending from the level of right frontal cirrus to near transverse cirri. Rarely (two of more than 50 specimens) two frontoventral rows present (Fig. 124c in Berger 1999). No frontoventral cirri originating from anlagen II–V arranged behind level of buccal vertex. Most specimens with three slightly enlarged cirri close to rear end of frontoventral row (problems with exact designation, see remarks). All cirri rather long, that is, 25 µm. Dorsal bristles about 5 µm, those of rear portion "also" 8–9 µm long[1]; arranged, as is usual for *Gonostomum*, in three (likely more or less bipolar) kineties. Three caudal cirri.

Korean population (Fig. 25f–j, Table 14): The reader is mainly referred to the illustrations and the morphometric characterisation. Only the life-data and other important features and/or data distinctly deviating from that of the type populations are

[1] The "also" would imply that the bristles in the rear portion are 5 µm *or* 8–9 µm long.

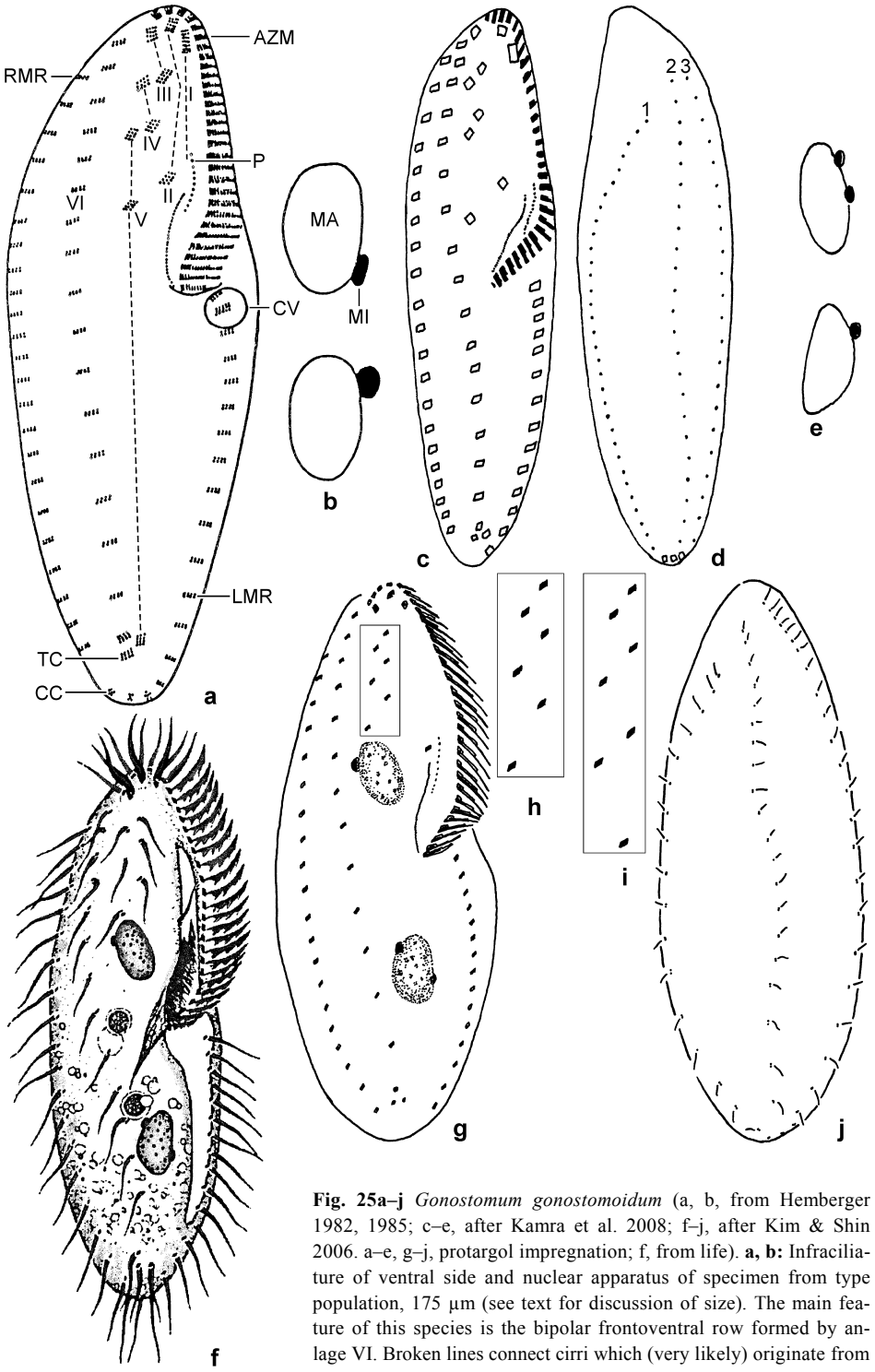

Fig. 25a–j *Gonostomum gonostomoidum* (a, b, from Hemberger 1982, 1985; c–e, after Kamra et al. 2008; f–j, after Kim & Shin 2006. a–e, g–j, protargol impregnation; f, from life). **a, b:** Infraciliature of ventral side and nuclear apparatus of specimen from type population, 175 µm (see text for discussion of size). The main feature of this species is the bipolar frontoventral row formed by anlage VI. Broken lines connect cirri which (very likely) originate from

mentioned. Body size 60–121 × 21–40 µm in life (n = 19?); ratio of body length to width roughly 3:1 in life and about 2.5:1 after protargol impregnation. Body outline elliptical, with both ends rounded; according to text, right posterior margin emarginate, a feature not clearly recognisable in the illustration (Fig. 25f). Body flexible, but non-contractile. Two oval macronuclear nodules with 3–5 spherical micronuclei nearby; chromatin bodies obviously of ordinary size. Contractile vacuole up to about 9 µm across; located at level of buccal vertex and with two distinct collecting canals (Fig. 25f); split in two small vesicles during diastole. Cytoplasm colourless, containing small (1.5–3.0 µm across), colourless fat globules mainly in posterior portion. For problem (presence/absence) with cortical granules, see remarks. Underneath pellicle many colourless, ellipsoidal (2–3 µm long) structures, likely mitochondria. Movement rapid, without peculiarities; creeping on bottom or freely swimming. Adoral zone occupies about 50% of body length, composed of 31 membranelles on average; largest membranelles 7–10 µm wide. Kim & Shin (2006) obviously confused endoral and paroral because according to the text the endoral is anterior to the paroral, which, however, contradicts their illustrations which shows the ordinary *Gonostomum*-pattern; specimen illustrated with 11 paroral cilia/basal bodies. Pharyngeal fibres 10–17 µm long. Frontoventral cirri formed by anlagen III–V arranged in (pseudo)pairs roughly forming a zigzag-pattern (Fig. 25g–i). Frontoventral row (incorrectly termed midventral row by Kim & Shin) composed of 14 cirri on average. Three "transverse" cirri not distinctly enlarged, triangularly arranged (for problems with this group, see remarks). Dorsal kinety 1 distinctly, kinety 2 slightly, and kinety 3 not shortened anteriorly; caudal cirri conspicuous because somewhat more extending beyond cell margin than marginal cirri. Dorsal bristles uniformly about 3–5 µm long, that is, bristles of rear portion not elongated as in type population.

Kamra et al. (2008) found only few specimens in their samples and therefore could not provide a detailed morphometry (Table 14). Mean body size of protargol-impregnated specimens 78 × 23 µm. Endoral composed of narrowly spaced cilia, commences about 26 µm behind anterior end of cell. Distance between individual cilia/basal bodies of paroral 0.5 µm. Cirral pattern of specimen illustrated agrees rather perfectly with that of type population (Fig. 25a, c).

Cell division: Hemberger (1982) illustrated three dividers (Fig. 124d–f in Berger 1999). He did not observe early stages, but supposed that these are similar to those of *Gonostomum affine*. Likely, the anlagen II–V of the proter and the opisthe originate from so-called primary primordia, that is, long streaks, which divide to form the anlagen (secondary primordia) for the proter (anterior portion) and opisthe (posterior

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← same anlage. **c–e:** Infraciliature of ventral and dorsal side and nuclear apparatus of Indian specimen, 75 µm. The cirral pattern matches perfectly that of the type population. **f:** Ventral view of Korean specimen, 111 µm. **g–j:** Infraciliature of ventral (g–i) and dorsal side and nuclear apparatus of specimens from Korean population, 100 µm. Rectangles surround frontoventral cirri. AZM = adoral zone of membranelles, CC = caudal cirri, CV = contractile vacuole, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = right marginal row, TC = transverse cirri, I–VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 158.

portion). The primary primordium for the frontoventral row originates in the central portion of the parental row (Fig. 124d, e in Berger 1999). The three frontal cirri, the cirrus behind the right frontal cirrus (III/2), the two anteriormost cirri (= frontoterminal cirri) and the rear portion (about five cirri) of the frontoventral row, and the three enlarged "transverse" are not involved in primordia formation. Especially the non-participation of cirrus III/2 is interesting because this cirrus usually forms anlage III of the proter in the oxytrichids (Table 4 in Berger 1999), other *Gonostomum* species (Table 15), and many other taxa, for example amphisiellids (*Lamtostyla australis*, Voß 1992, Fig. 31o, p in Berger 2008; *Lamtostylides edaphoni*, Petz & Foissner 1996, Fig. 64l in Berger 2008), taxa of unknown position as, for example, *Apourosomoida halophila* (Foissner et al. 2002a; Fig. 110c, d in Berger 2008), *Nudiamphisiella illuvialis* (Eigner & Foissner 1994; Fig. 120n in Berger 2008), *Vermioxytricha arenicola* (Foissner et al. 2002a; Fig. 126u, v in Berger 2008), *Hemiurosoma terricola* (Foissner et al. 2002a; Fig. 130n in Berger 2008), and some urostyloids (*Anteholosticha heterocirrata*, Hemberger 1982, Fig. 133g in Berger 2008). However, other taxa where cirrus III/2 is not involved in primordia formation are also known, for example, *Trachelostyla pediculiformis* (Fig. 1F, H in Shao et al. 2007) or *Anteholosticha monilata* (Hemberger 1982; Fig. 56c, d in Berger 2006a).

Occurrence and ecology: *Gonostomum gonostomoidum* is likely confined to terrestrial habitats of Eurasia because so far all records are from this part of the holarctis[1]. Type locality is the area north of the city of Bonn (Germany) where the River Sieg flows into the River Rhine; Hemberger (1982, p. 2; 1985) collected excrement of the common land snail *Deroceras reticulatum* (Kerney et al. 1983); likely the infusion was set up with distilled water. The Korean population was found in soil under an oak tree in Ulsan (35°36'59"N 129°27'07"E) in Mid-November 2003 (Kim & Shin 2006). Kamra et al. (2008) isolated *G. gonostomoidum* from soil collected in the Valley of Flowers (Himalayan regions, India), an about 88 km^2 large permafrost mountain area at an altitude of 3250–6750 m (exact location not described). The soil is permanently wet and Kamra et al. (2008) therefore supposed that for that reason only few specimens excysted with the non-flooded Petri dish method. Food not mentioned in original description and redescriptions; likely it ingests, inter alia, bacteria.

Gonostomum terrestre (Alekperov, 2005) comb. nov.
(Fig. 26a, b)

2005 ***Trachelochaeta terrestris* sp. n.** – Alekperov, Atlas of free-living infusoria, p. 219, Fig. 69$_{3, 4}$, Plate 22 2 (Fig. 26a, b; original description; no formal diagnosis provided; type slides ["S-P-No2"] likely deposited in the private collection of Ilham Alekperov).

[1] According to Foissner (1998, p. 210), *Trachelochaeta gonostomoida* is an element of the neotropis (Central and South America). However, somewhat later he (Foissner 2000a, p. 260) recognised that the snail faeces in which the type population lived was collected near the German city of Bonn (Hemberger 1982, p. 2; Berger 1999, p. 393).

Nomenclature: No derivation of the species-group name is given in the original description. The name *terrestr·is*, *-is*, *-e* (Latin adjective [m, f, n]; living on the land or in the soil; Hentschel & Wagner 1996, p. 576) refers to the habitat where the species was discovered. *Trachelochaeta* is feminine (see p. 300), *Gonostomum* is neuter (see above); thus, the ending of the species-group name has to be changed to *G. terrestre* nom. corr.

Remarks: *Gonostomum terrestre* is a difficult species because the Russian description is based on wet silver nitrate impregnation and likely contains some irregularities and uncertainties (Fig. 26a, b). The cirral pattern closely resembles that of *Neowallackia petergofi*, which has the same type locality (p. 298). However, this species lacks transverse cirri and has only three dorsal kineties (vs. likely five in *G. terrestre*). A detailed redescription (live observation, infraciliature and morphometry after protargol impregnation) of both species is urgently needed to confirm them. When the five dorsal kineties of *G. terrestre* can be approved, then a synonymy with the also rather similar *G. gonostomoidum* can be excluded (for a more detailed comparison, see *G. gonostomoidum*). According to the illustration, the present species has only five frontal-ventral-transverse cirri anlagen (against six in other *Gonostomum* species). Further studies will show whether this is assumption is correct or a misinterpretation of the cirral pattern.

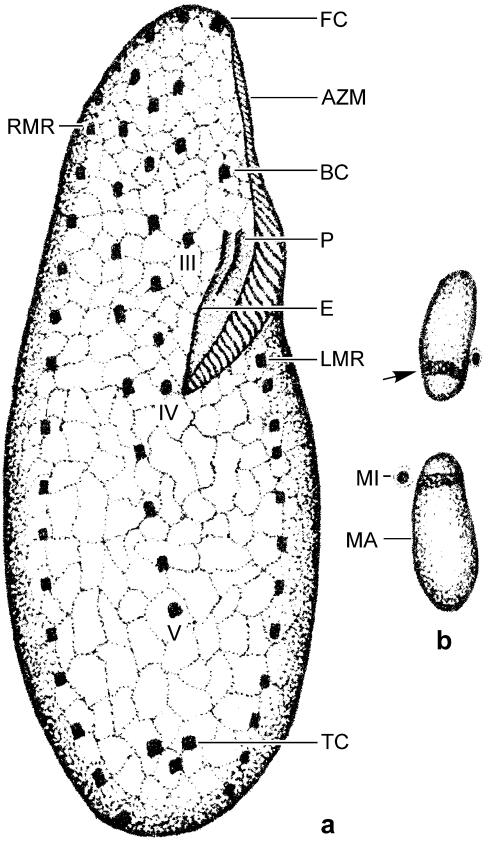

Fig. 26a, b *Gonostomum terrestre* (from Alekperov 2005. Wet silver nitrate impregnation). Infraciliature of ventral side and nuclear apparatus, 28 µm. Arrow marks replication band. The fine meshes in (a) are the silverline system, which is of no taxonomic value in the hypotrichs, at the present state of knowledge. Perhaps *G. terrestre* is identical with *Neowallackia petergofi* (Fig. 55a, b). AZM = adoral zone of membranelles, BC = buccal cirrus, E = endoral, FC = left frontal cirrus, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = right marginal row, TC = transverse cirri (perhaps one of them is a pretransverse ventral cirrus), III–V = frontoventral rows. Page 164.

Morphology: As mentioned above, the original description of *G. terrestre* is in Russian. Thus, the following paragraph is mainly based on the illustration. The micrograph in Alekperov (2005, Plate 22, Fig. 2) basically agrees with the illustration,

but details are not clearly recognisable. Body length 30–45 µm (in life?), specimen illustrated only 28 × 11 µm. Two ellipsoidal macronuclear nodules with each one micronucleus. Contractile vacuole not illustrated, presence/absence of cortical granules likely not mentioned.

Oral apparatus obviously gonostomatid; adoral zone occupies 47% of body length in specimen illustrated; composed of 45–50 membranelles, a rather high value for such a small species. Paroral short, endoral commences at same level as paroral and extends to proximal end of adoral zone; no details recognisable.

Cirral pattern as shown in Fig. 26a. Three frontal cirri along anterior cell margin. One buccal cirrus ahead of undulating membranes. Three cirral rows which become successively longer from left to right; row III composed of three cirri (frontal cirrus not included), ends about at level of anterior end of undulating membranes; row IV composed of six cirri, terminates close to buccal vertex; row V made of 10 cirri, extends to 74% of body length in specimen illustrated. Three transverse cirri (perhaps one of them is a pretransverse ventral cirrus). Right marginal row commences about at same level as frontoventral rows, composed of about 17 cirri, terminates, like left row, somewhat subterminally. Left marginal row composed of 12 cirri.

No illustration of dorsal infraciliature provided; likely five dorsal kineties (which would be untypical for *Gonostomum*), composed of 14–18 bristles. I do not know whether or not caudal cirri are present.

Occurrence and ecology: Likely confined to terrestrial habitats. *Gonostomum terrestre* obviously has the same type locality as *Neowallackia petergofi* (p. 298), that is, the Petergof Park near the city of St. Petersburg (Russia) where Alekperov (2005) discovered it in soil. No further records published.

Gonostomum sp. 1 in Shin (1994)
(Fig. 27a–c, Table 14)

1994 ***Gonostomum* sp. 1** – Shin, Dissertation, p. 113, Fig. 16a–C, Table 15 (Fig. 27a–c; description of Korean population; the "holotype" slide [accession number: USNM # 43205] is deposited in the International Protozoan Type slide Collection, Smithsonian Institution, Washington DC, USA; a "paratype" is deposited in the Department of Molecular Biology, Seoul National University, Korea; see nomenclature).

Nomenclature: Shin (1994) did not provide a species-group name. In spite of that, he designated the slide, which he obviously deposited in the Smithsonian Institution, as holotype slide. Whether or not an undescribed species can have a holotype needs a detailed analysis, especially when further studies show that "*Gonostomum* sp. 1" is a valid species.

Remarks: This population has, on average, two frontal-ventral-transverse cirri more than an 18-cirri hypotrich. The "extra" pseudo-pair obviously results from an additional (seventh) frontal-ventral-transverse cirri anlage. This feature and a full set of pretransverse ventral and transverse cirri is not yet described for *G. affine* so that

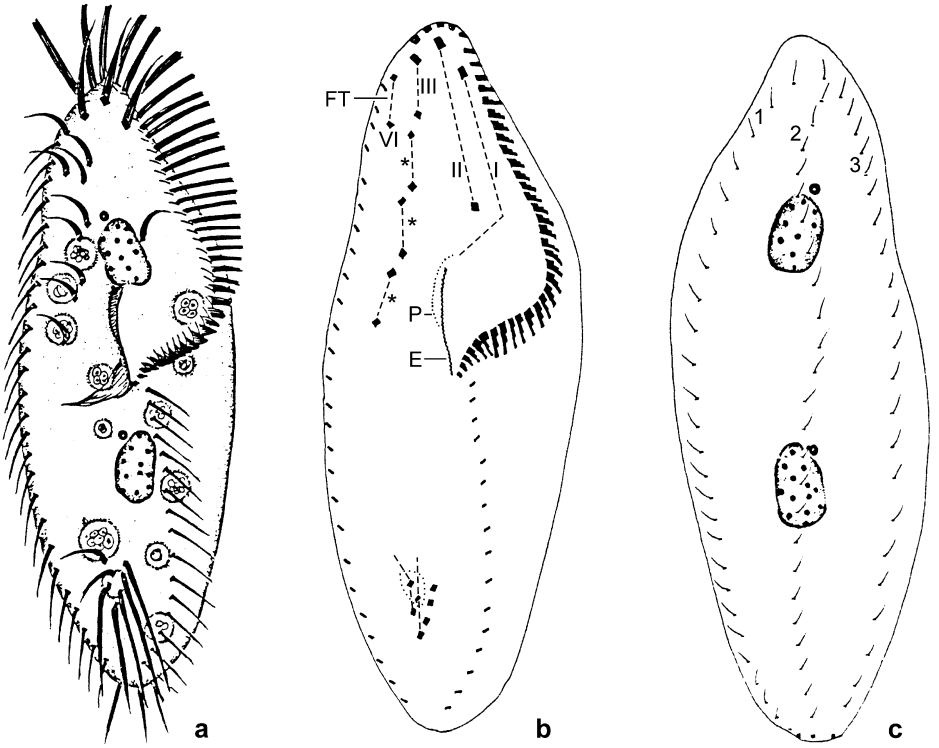

Fig. 27a–c *Gonostomum* sp. 1 (from Shin 1994. a, from life; b, c, protargol impregnation). **a:** Ventral view, 146 µm. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus (of same specimen?), b, c = 130 µm. Broken lines connect cirri which (very likely) originated from same anlage; one of the three anlagen marked by an asterisk is very likely an additional (seventh) anlage. Pretransverse ventral cirri encircled. E = endoral, FT = frontoterminal cirri, P = paroral, I–VI = frontal-ventral-transverse cirri anlagen, 1–3 = dorsal kineties. Page 166.

it seems wise to separate such a form from the type species. Further populations, preferable from the same area, should be studied to show whether or not this cirral pattern is stable. Since Shin's (1994) dissertation is not widely distributed, I include the data in the present review. Shin studied 15 live specimens and 25 protargol-impregnated individuals so that the morphometric data are convincing.

Morphology: Body 132–155 × 48–64 µm in life. Body outline elongate to long oval, anterior and posterior end narrowed; left anterior margin oblique (Fig. 27a). Body soft and flexible. Two ellipsoidal macronuclear nodules about in midline. Two spherical micronuclei. Contractile vacuole globular, as is usual about in mid-body near left cell margin. Presence/absence of cortical granules not mentioned. Up to 18 food vacuoles (7 µm across) scattered throughout cell. Movement rapid, changing direction frequently.

Adoral zone occupies about 52% of body length. Buccal field deep. Paroral composed of about 24 cilia (note that Shin confused endoral and paroral).

Cirral pattern as shown in Fig. 27b and characterised in Table 14. Frontal cirri slightly enlarged, arranged as in other *Gonostomum* species. Buccal cirrus distinctly ahead of undulating membranes. Three oblique pseudopairs of frontoventral cirri likely due to an additional frontal-ventral-transverse cirri anlage (Fig. 27b). Two frontoterminal cirri left of anterior portion of right marginal row. Two pretransverse ventral cirri and five subapical transverse cirri arranged in hook-shaped pattern. Right marginal row commences at level of left frontal cirrus, terminates, like left row, almost at cell end; left marginal row begins close to buccal vertex.

Dorsal bristles about 5 µm long (however, some of them shortened according to Shin), arranged – as in other *Gonostomum* species – in three bipolar kineties. Invariably three caudal cirri (Fig. 27c).

Occurrence and ecology: Shin (1994) found this population in soil samples (soil moss-covered) from ordinary ricefields (and a brooklet?; see Shin 1994, p. 258, "st. 17") in Misan-myon (38°02'N 127°01'E), Yonchon-gun, Kyonggi-do near Seoul, Korea. Food not described.

Incertae sedis in *Gonostomum*

Urosoma macrostomum Gellért, 1957
(Fig. 28a)

1957 ***Urosoma macrostoma* n. sp.** – Gellért, Annls Inst. biol. Tihany, 24: 21, Fig. 7 (Fig. 28a; original description; no formal diagnosis provided and likely no type material available).

1972 ***Trachelostyla macrostoma* (Gellért, 1957)** – Borror, J. Protozool., 19: 15 (revision of hypotrichs; combination with *Trachelostyla*).

1974 ***Urosoma macrostoma* Gellért** – Stiller, Fauna Hung., 115: 118, Fig. 71C (Fig. 28a; guide to Hungarian hypotrichs).

1999 ***Urosoma macrostoma* Gellért** – Berger, Monographiae biol., 78: 370, Fig. 118a (Fig. 28a; classified as synonym of *G. affine*).

2001 ***Urosoma macrostoma* Gellért, 1957** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 99 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: No derivation of the species-group name is given in the original description and the review by Berger (1999). The name *macrostom·us, -a, -um* (Latin adjective [m; f; n]; literally big-mouthed, having a large, long mouth) is a composite of the Greek adjective *makros* (large) and the Greek noun *to stoma* (mouth), referring to the large oral apparatus, respectively, adoral zone (relative length 37%). Since the generic assignment is very uncertain (see remarks), I use the basionym in the heading. *Urosoma* is neuter (ICZN 1999, Article 30.1.2; Aescht 2001, p. 304); thus, the correct spelling is *Urosoma macrostomum* nom. corr. For derivation of *Urosoma*, see Berger (2008, p. 614).

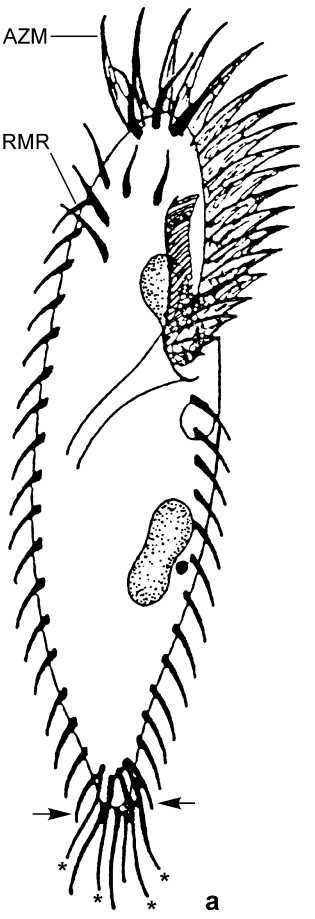

Fig. 28a *Urosoma macrostomum* (after Gellért 1957. Sublimate-glycerine-alcohol fixation and opalblue preparation after Bresslau). Infraciliature of ventral side and nuclear apparatus, 75 µm. Arrows mark rear end of marginal rows. Asterisks denote transverse cirri; together with the three caudal cirri they form a rather dense tuft. AZM = distal end of adoral zone of membranelles, RMR = anterior end of right marginal row. Page 169.

Remarks: *Urosoma macrostomum* was synonymised with *G. affine* by Berger (1999), however, without foundation. The following features support the proposed synonymy: (i) body size (70 µm) and shape; (ii) adoral zone more or less gonostomatid; (iii) postoral ventral cirri in postoral area lacking; and (iv) number of frontoventral cirri rather low, a feature also known from "true" *G. affine* populations. By contrast, the long paroral composed of many, rather densely spaced cilia opposes a synonymy with *G. affine* and even a classification in *Gonostomum*. In the *Gonostomum* species described by Gellért (1942, 1956a, 1957), the paroral is also relatively long, but the cilia are more widely spaced, indicating that Gellért knew about this characteristic feature (Fig. 17a; Fig. 118b, f–h in Berger 1999).

The original assignment to *Urosoma* is very likely also incorrect because *Urosoma* species usually also have a rather short paroral and the postoral ventral cirri are behind the buccal vertex (for review, see Berger 1999, p. 396). *Urosoma macrostomum*, however, lacks postoral ventral cirri at all, that is, has them neither behind nor right of the adoral zone. *Urosoma similis* (Foissner, 1982) Berger, 1999 (basionym *Perisincirra similis*; for review, see Berger 1999, p. 397), which fulfils this criterion, was transferred to *Hemiurosoma* by Foissner et al. (2002a, p. 835), a genus, which is – like *Urosoma* – very likely a non-oxytrichid dorsomarginalian because a dorsomarginal kinety is present, but a dorsal kinety fragmentation is lacking (for review of *Hemiurosoma*, see Berger 2008, p. 614). However, *Hemiurosoma similis* is larger (120–180 × 18–28 µm) and the relative length of the adoral zone is distinctly lower than in *U. macrostomum* (about 20% vs. 37%). Further, the paroral of *Hemiurosoma* species is very similar to that of *Gonostomum*. Since the dorsal kinety pattern of *U. macrostomum* is not known, a classification in *Hemiurosoma* would be as uncertain as the synonymy with *G. affine*. Anyhow, the arrangement of the frontoventral cirri is reminiscent of the *Urosoma*-pattern (Fig. 19a in Berger 1999), indicating that *Urosoma macrostomum* is more closely related to *Hemiurosoma similis* than to *Gonostomum*.

Borror (1972) has assigned *U. macrostomum* to *Trachelostyla*. However, the trachelostylids are a marine group and have a distinctly narrowed (cephalised) anterior body portion, strongly indicating that this generic assignment is incorrect (Berger 2008, p. 475). Foissner (1998, p. 210) considered it as valid soil species.

Buitkamp (1977, p. 125) suggested synonymy with *Urosomoida agilis* (Engelmann, 1862) Hemberger in Foissner, 1982. Admittedly, this species is very similar in shape, but it is larger (80–160 × 30–35 µm), has a shorter adoral zone (20–25%), and three postoral ventral cirri behind the buccal vertex (Fig. 110a–j in Berger 1999). Thus, I do not agree with the synonymy proposed by Buitkamp (1977).

As a consequence of the uncertain systematic status, I remove *U. macrostomum* from the synonymy of *G. affine* and classify it as incertae sedis in *Gonostomum*, however, without transferring it to this genus. The maintenance of the original assignment in *Urosoma* or a transfer to another genus (*Hemiurosoma*, *Urosomoida*, *Trachelostyla*) are as unsatisfactory as the synonymy with *G. affine*. Soil samples from the type locality (coniferous soil from north-east Hungary) have to be studied to show whether or not this species exists. It is not impossible that it is a valid taxon, because recently Vd'ačný & Tirjaková (2006) found a new *Gonostomum* species in Eastern Europe.

Morphology: The original description is in Hungarian and therefore I got most data from the illustration. Likely, the description is based – as in other descriptions provided by Gellért – on a single specimen. Body length 70 µm; length:width ratio of specimen illustrated 2.7:1 (Fig. 28a). Body outline spindle-shaped, that is, widest in mid-body, anterior end broadly, posterior end narrowly rounded. Two dumbbell-shaped macronuclear nodules left of midline, each one in anterior and posterior body half. One micronucleus attached to each(?) macronuclear nodule. Contractile vacuole at 42% of body length close left cell margin. Presence/absence of cortical granules and movement very likely not described. Adoral zone gonostomatid, occupies 37% of body length, and composed of 19 membranelles in specimen illustrated. Buccal field moderately wide, right margin bordered by rather long paroral[1] composed of closely spaced cilia, indicating that it does not belong to *Gonostomum* (see remarks for detailed discussion). Specimen illustrated with 12 frontal-ventral-transverse cirri, namely, three slightly enlarged frontal cirri forming slightly curved pseudorow along anterior end; one buccal cirrus close to anterior end of paroral (the buccal cirrus is rather far anteriorly, which is also a difference to *G. affine*); one cirrus (III/2) behind right frontal cirrus; three frontoventral cirri forming short row left of anterior portion of right marginal row (these three cirri and cirrus III/2 are more or less distinctly arranged in the so-called *Urosoma*-pattern; Fig. 19a in Berger 1999); four transverse cirri distinctly projecting rear body end (it cannot be excluded that one or two pretransverse ventral cirri are included); postoral ventral cirri lacking. Right marginal row commences about at level of buccal cirrus, ends slightly subterminally, composed of 18 cirri in specimen illustrated. Left marginal row com-

[1] It is difficult to estimate the number of paroral cilia from Fig. 28a; there are about 25–30 cilia illustrated; however, note that this must not be overinterpreted.

mences slightly behind buccal vertex, ends about at level of transverse cirri, made up of 13 cirri. Length and arrangement of dorsal bristles likely not mentioned. Three caudal cirri forming, together with transverse cirri, rather dense tuft at rear cell end.

Occurrence and ecology: Gellért (1957, p. 32) studied soil samples from various habitats in Hungary. Unfortunately, he did not name the individual localities in the German summary. According to Gellért (1957, p. 13, Table 1) and Stiller (1974, p. 118), *Urosoma macrostomum* was discovered in a soil sample from a coniferous forest near the village of Boldogkőváralja, about 35 km north-east of the city of Miskolc. Interestingly, this is also the type locality of the various *Gonostomum* species described by Gellért (details, see *G. affine*). To check the validity of *Urosoma macrostomum*, soil samples from this area should be examined. No further records published. Feeds on algae (Gellért 1957); Foissner (1998, p. 210) mentioned detritus as food.

Insufficient redescription

***Gonostomum strenuum* (Engelmann, 1862)** – Çapar, 2007, Hacettepe J. Biol. Chem., 35: 48, Fig. 5a–c (Fig. 29a–c). Remarks: The description and illustrations differ from the authoritative descriptions in two main features, namely, (i) the frontoventral row is not extending beyond the level of the buccal vertex and (ii) frontoterminal cirri are neither illustrated nor mentioned. Whether the latter cirral group is lacking, overlooked, or misinterpreted is not known. A validation of the identification would make the characterisation of *G. strenuum* again rather imprecise; thus, the Turkish population is classified as insufficient redescription. Since one cannot exclude that it represents a heretofore undescribed species, a brief characterisation is provided: body size 70–85 × 20–25 µm (in life?); body outline elliptical. Two macronuclear nodules, 12–15 ×

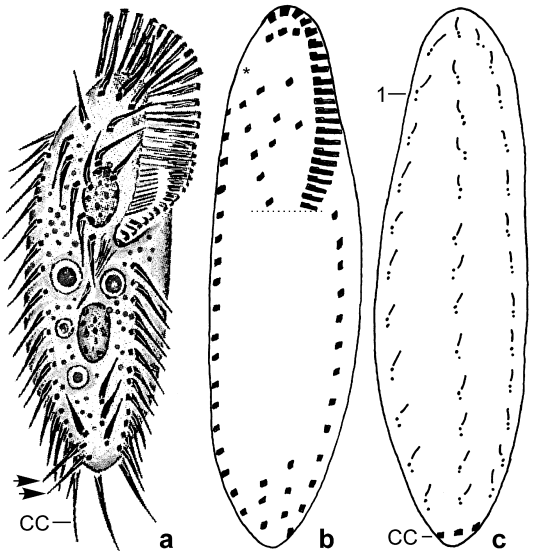

Fig. 29a–c Insufficient redescription of *Gonostomum strenuum* (after Çapar 2007. a, from life; b, c, protargol impregnation). **a:** Ventral view, about 80 µm. Arrows mark "posteriorly located two transverse cirri". **b, c:** Infraciliature of ventral and dorsal side (of same specimen?), 76 µm. Dotted transverse line shows that the frontoventral row does not extend beyond the buccal vertex, and about four frontoterminal cirri should be arranged in the area marked with an asterisk; both deviations indicate that the identification as *G. strenuum* is incorrect (further details, see text). CC = caudal cirri, 1 = dorsal kinety 1. Page 171.

5–8 µm; one micronucleus attached to each macronuclear nodule. Contractile vacuole obviously in ordinary position, that is, near left cell margin at level of buccal vertex; up to 8–9 µm across. Cortical granules difficult to recognise; no details provided. Adoral zone gonostomatid, occupies about 40% of body length; undulating membranes neither described nor illustrated. All cirri of equal thickness. Cirral pattern, see Fig. 29b; according to the somewhat imprecise description the following cirri are present: three frontal cirri, 8–9 ventral cirri (not extending beyond level of buccal vertex!), one buccal cirrus, two pretransverse cirri (in the paper mislabelled as transverse cirri), three transverse cirri; in addition two transverse cirri close to the rear end are present. Right marginal row distinctly shortened anteriorly (misobservation?); composed of 18 cirri in specimen illustrated (Fig. 29b); left marginal row composed of 13 cirri, extends close to rear cell end. Three dorsal kineties, each with one caudal cirrus (Fig. 29c). Found in a soil sample from the "flooded" zone (however, the sample was taken when the area was not flooded) of the Gelingüllü Dam Lake (39°36'30"N 35°03'20"E), south of Yozgat Province, Central Anatolia Region, Turkey (see also Çapar 2007a, p. 208).

Paragonostomum Foissner, Agatha & Berger, 2002

2002 ***Paragonostomum* nov. gen.**[1] – Foissner, Agatha & Berger, Denisia, 5: 819 (original description). Type species (by original designation): *Paragonostomum caudatum* Foissner, Agatha & Berger, 2002.

2008 ***Paragonostomum* Foissner, Agatha & Berger, 2002** – Lynn, Ciliated protozoa, p. 361 (familial revision of ciliates).

Nomenclature: *Paragonostomum* is a composite of the Greek prefix *para-* (beside) and the genus-group name *Gonostomum* (see there for derivation) meaning a ciliate related to *Gonostomum* (Foissner et al. 2002a). Like *Gonostomum*, neuter gender (Foissner et al. 2002a; Aescht 2001, p. 284).

The name *Paragonostomum* was published for the first time in Foissner (2000a, p. 259; as *P. caudatum*, with a hint that the description is in preparation) in a species list. However, since most conditions necessary for publication are not met, for example, type species not fixed and no description provided (ICZN 1999, chapter 4), the names *Paragonostomum* and *P. caudatum* have not been made available in this paper.

Characterisation (A = supposed apomorphy): Adoral zone of membranelles and undulating membranes in *Gonostomum*-pattern. Paroral continuous [*Paragonostomum (Paragonostomum)*] or bipartite [*Paragonostomum (Bigonostomum)*]. Posterior body portion more or less tail-like (A), except for *P. simplex* and *P. minuta*.

[1] Foissner et al. (2002a) provided the following diagnosis: Oxytrichinae without transverse cirri. Adoral zone of membranelles, undulating membranes, and ontogenesis in *Gonostomum* pattern. Posterior body portion more or less distinctly tail-like. Frontoventral cirri and frontoterminal cirri in Y-like pattern or single row. 1 right and left marginal row. 3 dorsal kineties.

Frontal-ventral cirri originate from five anlagen because anlage IV (or V?) lacking. Three frontal cirri with left cirrus somewhat displaced posteriad. One buccal cirrus. One cirrus (III/2) behind right frontal cirrus. Cirri of anlage V (or IV; frontoventral row) and VI (frontoterminal cirri) form two rows or single row (*P. rarisetum*). Pretransverse ventral and transverse cirri lacking (A?). One left and one right marginal row. Three bipolar dorsal kineties. Presence or absence of caudal cirri not yet clearly known (likely present). Terrestrial.

Additional characters: Body flexible, not distinctly contractile; macronuclear nodules slightly left of midline; cortical granules lacking in tailed species, present in *P. simplex* and *P. minuta*, whose assignment to *Paragonostomum* is, however, uncertain; feeds mainly on bacteria, ocassionally on small algae; cirri mainly fine; dorsal bristles 3–5 µm long.

Remarks: We established *Paragonostomum* for *Gonostomum*-like species without transverse cirri and a conspicuous tail (Foissner et al. 2002a). Some *Gonostomum affine* specimens also lack transverse cirri, but usually two or more transverse cirri are present in the type species (for review, see p. 68 and Berger 1999, p. 369). The cirri on the tail are minute, that is, sometimes composed of only three cilia and their exact arrangement is often difficult to recognise. Thus, we could not unequivocally decide whether these are caudal or marginal cirri. Therefore this important feature was not included in the diagnosis by Foissner et al. (2002a). Detailed cell division date are needed for a correct interpretation of the tail ciliature in *Paragonostomum*.

The interphasic cirral pattern of *P. caudatum*, *P. multinucleatum*, and *P. binucleatum* indicates that only five frontoventral cirri anlagen are present (Fig. 30i, 33c, 35e). The loss of one anlage is confirmed by a late divider of *P. rarisetum* (Fig. 32e). The frontoventral cirri of *P. multinucleatum* and *P. binucleatum* are basically arranged as in *Gonostomum affine*, except that one of the two cirral pairs formed by anlage IV or V is lacking (cp. Fig. 3a, 33c, 35e, 36k). The question is which of the two anlagen – IV or V – has been lost in the stem-line of *Paragonostomum*? In *Gonostomum* the frontal-ventral cirri anlagen are formed from so-called primary primordia (p. 58, Table 15), and very likely the same is true for *Paragonostomum*. In many hypotrichs, anlage VI – which produces the frontoterminal cirri – originates from parental cirri of anlage V (Table 4 in Berger 1999). Thus, one can conclude that in these species anlage V must be present when frontoterminal are formed. However, anlage VI is formed de novo in *Gonostomum* (Table 15), so that this conclusion cannot be made in the *Gonostomum/Paragonostomum* group. Parental cirri formed by anlage VI are usually ontogenetically inactive (for review, see Berger 1999; Foissner et al. 2002a). From the arrangement of the cirri in the interphasic specimens it is not possible to conclude whether anlage IV or V is lacking in *Paragonostomum* because the rearmost cirral pair present in *P. multinucleatum* (Fig. 33c, e, i, j) and *P. binucleatum* (Fig. 35e, f) is in a position between that of the pairs formed by anlagen IV and V in *Gonostomum* (Fig. 36k). In *P. rarisetum*, the cirri of anlage VI (frontoterminal cirri) form a continuous row with the cirri produced by the

anlage left of it (Fig. 32a, c, e). This mixed row is reminiscent of the median cirral row of the amphisiellids (for review, see Berger 2008). The amphisiellid median cirral row is usually formed by cirri of the anlagen VI (form anterior portion) and V (form posterior portion). Presumed that this detail is homologous in the amphisiellids and *P. rarisetum* one could conclude that anlage V is present and anlage IV has been lost in *Paragonostomum*. However, further analyses have to be employed to clarify the question finally.

The four tailed species included in *Paragonostomum* differ in the nuclear apparatus, the arrangement of the frontoventral cirri, some morphometrics of the ciliature, and the structure of the paroral, which is bipartite in *P. binucleatum* and *P. multinucleatum* (e.g., Fig. 33e, f, j), but more or less continuous in the type species and *P. rarisetum* (e.g., Fig. 30i). The first group has fewer frontoventral cirri than the second, indicating that within *Paragonostomum* two groups evolved. Usually, conspicuous details of the undulating membranes are used to characterise genera, for example, *Notohymena* Blatterer & Foissner, 1988 and *Steinia* Diesing, 1866 (for review, see Berger 1999). In the present case, I use the difference to divide *Paragonostomum* into two subgenera, namely *P. (Paragonostomum)* and *P. (Bigonostomum)*. Of course molecular analyses should be made to show whether or not this morphological differences are also conserved at the (analysed) molecular level. However, only severely determined populations must be used!

Foissner et al. (2005) described *P. simplex*, which also lacks transverse cirri, but which has no tailed body. The cirral pattern of this species indicates that it is formed from six anlagen (Fig. 36j) against five in the tailed species (Fig. 30i, 33e). W. Foissner, who made the description of *P. simplex*, found some dividers, but did not mention this detail in the text. So far I had no time to reinvestigate this detail in the slides deposited so that this uncertainty remains. For that reason I classify *P. simplex* only as incertae sedis in *Paragonostomum* and do not include details of this species in the characterisation above. When division data show that the frontal-ventral ciliature is formed from six (I–VI) anlagen (Fig. 36j), then *P. simplex* should be classified in a new genus; if it is formed – as in the other species – from five anlagen, then it has to be assigned to the nominotypical subgenus *P. (Paragonostomum)*, because the paroral is continuous.

Kamra et al. (2008) discovered two acaudate *Paragonostomum* species in the soil of an Indian national park. One species very certainly does not belong to the present genus, but to *Neowallackia* (see species misplaced below).

Just recently, Lynn (2008) classified *Paragonostomum* in the Trachelostylidae (for review of this group, see Berger 2008), because he submerged the gonostomatids in the trachelostylids.

Species included in *Paragonostomum* (alphabetically arranged basionyms are given): Already seven species have been assigned to the "young" genus *Paragonostomum*. However, only the four species described by Foissner et al. (2002a) fit the genus criteria defined in the original description. The three species described by Foissner et al. (2005) and Kamra et al. (2008) lack the characteristic tail and have, in

contrast to the tailed species, cortical granules. *Paragonostomum ghangriai* is very similar to *Neowallackia franzi* and is therefore classified in this new genus. By contrast, the original classification of *P. simplex* and *P. minuta* are preliminary retained, but they are classified as species incertae sedis. (1) *Paragonostomum binucleatum* Foissner, Agatha & Berger, 2002a; (2) *Paragonostomum caudatum* Foissner, Agatha & Berger, 2002a; (3) *Paragonostomum multinucleatum* Foissner, Agatha & Berger, 2002a; (4) *Paragonostomum rarisetum* Foissner, Agatha & Berger, 2002a. Incertae sedis: (5) *Paragonostomum minuta* Kamra, Kumar & Sapra, 2008; (6) *Paragonostomum simplex* Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005.

Species misplaced in *Paragonostomum*: The following species very likely does not belong to *Paragonostomum*.

Paragonostomum ghangriai Kamra, Kumar & Sapra, 2008. Remarks: The infraciliature of this species matches that of *Neowallackia franzi* more or less perfectly. Thus, it is transferred to *Neowallackia* (p. 295).

Key to species and subgenera of *Paragonostomum* and similar species

If you cannot identify your specimen/population with the key below, see also keys to *Wallackia* (p. 206), *Neowallackia* (p. 280), or *Gonostomum* (p. 58).

1 Body more or less distinctly tailed (e.g., 30a, 32a, 33a, 35a, 37a–c). **2**
- Body not tailed (e.g., Fig. 36a, 37d, e, 38a, 52a). **5**

2 Paroral bipartite (e.g., Fig. 33e, f, i, j). . . . . *Paragonostomum (Bigonostomum)* (p. 184)
- Paroral continuous (e.g., Fig. 30a, b, h, i). **3**

3 Distinct transverse cirri present (Fig. 22a–j). . . *Gonostomum namibiense* (p. 140)
- Transverse cirri lacking or very indistinct (e.g., Fig. 30a, 42a). **4**

4 Frontoventral cirri basically confined to area right of adoral zone of membranelles (Fig. 30h, i, 32a). . . . . *Paragonostomum (Paragonostomum)* (p. 176)
- Rightmost frontoventral cirral row extends to near rear body end (Fig. 42a, b, f). . . . . *Wallackia elegans* (p. 227)

5 (1) Frontoventral cirri basically confined to area right of adoral zone of membranelles (Fig. 36a, d). . . . . *Paragonostomum simplex* (p. 193)
- Rightmost or rightmost two frontoventral rows extend distinctly beyond level of buccal vertex or to near rear cell end (Fig. 38a, 53a). **6**

6 Body length about 75 µm in life; two frontoventral rows; on average 11–18 macronuclear nodules (Fig. 52a–f, 53a, b, 54a–c). . . . . *Neowallackia franzi* and *N. ghangriai* (p. 281, 295)
- Body length about 33 µm in life; one frontoventral row; 7–8 macronuclear nodules (Fig. 38a–c). . . . . *Paragonostomum minuta* (p. 204)

Paragonostomum (Paragonostomum) Foissner, Agatha & Berger, 2002 stat. nov.

2002 ***Paragonostomum* nov. gen.**[1] – Foissner, Agatha & Berger, Denisia, 5: 819 (original description). Type species (by original designation): *Paragonostomum caudatum* Foissner, Agatha & Berger, 2002.

Nomenclature: See genus section. Nominotypical subgenus of *Paragonostomum*.

Characterisation (A = supposed apomorphy): *Paragonostomum* with continuous paroral. Frontoventral row usually composed of four or more cirri (A?; cirrus III/2 included; frontoterminal cirri not included).

Type species (same as for *Paragonostomum*; ICZN 1999, Article 67.1.1): *Paragonostomum caudatum* Foissner, Agatha & Berger, 2002a.

Remarks: For a foundation of the subgenus, see remarks at genus section.

Species included in *Paragonostomum (Paragonostomum)* (alphabetically arranged basionyms are given): (1) *Paragonostomum caudatum* Foissner, Agatha & Berger, 2002a; (2) *Paragonostomum rarisetum* Foissner, Agatha & Berger, 2002a.

Key to *Paragonostomum (Paragonostomum)* species

Separation of the two species included is rather difficult and needs protargol impregnation.

1 Frontoventral row not in line with frontoterminal cirri; in total about 10 frontoventral cirri (frontoterminal cirri and cirrus III/2 included); on average about 19 adoral membranelles (Fig. 30h, i, l). . . . . *Paragonostomum (Paragonostomum) caudatum* (p. 176)

\- Frontoventral row more or less in line with frontoterminal cirri; in total about 6–7 frontoventral cirri (frontoterminal cirri and cirrus III/2 included); on average about 15 adoral membranelles (e.g., Fig. 32a, c). . . . . *Paragonostomum (Paragonostomum) rarisetum* (p. 183)

Paragonostomum (Paragonostomum) caudatum Foissner, Agatha & Berger, 2002 stat. nov.

(Fig. 30a–l, 31a–c, 37a, b, Table 16)

2002 ***Paragonostomum caudatum* nov. spec.**[2] – Foissner, Agatha & Berger, Denisia, 5: 820, Fig. 178a–l, 381s, t, Table 158 (Fig. 30a–l, 37a, b; original description; one holotype slide [accession number

[1] For the diagnosis provided by Foissner et al. (2002a), see genus section.

[2] Foissner et al. (2002a) provided the following diagnosis: Size about 85 × 20 µm in vivo. Lanceolate with conspicuous tail occupying about 25% of body length. 2 macronuclear nodules. On average 19 right marginal, 11 left marginal, and 4 frontoterminal cirri; frontoterminal and frontoventral cirral rows distinctly separate, the latter composed of an average of 6 cirri and ending at 30% of body length; 1 buccal

2002/733] and four paratype slides [2002/734–737] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Foissner et al. 2002a, p. 41; Aescht 2008, p. 148; see nomenclature).

2007 ***Paragonostomum caudatum* Foissner, Agatha and Berger, 2002** – Çapar, Hacettepe J. Biol. Chem., 35: 51, Fig. 11a–c (Fig. 31a–c; brief description of a Turkish population).

Nomenclature: The species-group name *caudat·us*, *-a*, *-um* (Latin adjective [m; f; n]; having a tail) refers to the conspicuous tail, a main feature of this species (Foissner et al. 2002a). Type species of *Paragonostomum* and *P. (Paragonostomum)*. By mistake, Foissner et al. (2002a, p. 41) wrote that three paratypes have been deposited in the Museum in Linz.

Remarks: *Paragonostomum caudatum* has a very conspicuous tail, which is likely due to body elongation because the ordinary ratio of length of adoral zone to body length of 50% in *Gonostomum* is obtained only when the tail is omitted (Fig. 30a; Foissner et al. 2002a). *Paragonostomum rarisetum*, which also has only two macronuclear nodules, has a lower number of frontoventral cirri, which form a mixed row with the frontoterminal cirri (Fig. 32a, c). It differs from the binucleate *P. binucleatum* by the higher number of frontoventral cirri (10 vs. 5), and the tail (conspicuous vs. indistinct; Fig. 35a, e). Because of the bipartite paroral, *P. binucleatum* is classified in the subgenus *P. (Bigonostomum)*. *Gonostomum namibiense*, which also has two macronuclear nodules and a distinct tail, has – as is usual for *Gonostomum* – distinct transverse cirri (Fig. 22a–g). *Paragonostomum multinucleatum* and *P. simplex* have seven and 10 macronuclear nodules on average, respectively (Tables 16, 17).

Çapar (2007) described a Turkish population of *P. caudatum*. Interestingly, she mentioned, like Foissner et al. (2002a), 7–12 paroral cilia, but did not illustrated the paroral in the protargol-impregnated specimen (Fig. 31b).

Morphology: The description below is based on the type population, unless otherwise indicated. Some additional data of the population studied by Çapar (2007b) are mentioned separately.

Body size 70–100 × 15–25 µm in life, usually about 85 × 20 µm; length:width ratio of trunk 3.0–4.6:1, 3.6:1 on average in protargol preparations (Table 16). Body clavate due to lanceolate to ellipsoidal trunk and cylindroidal tail occupying about 25% of body length in live and protargol preparations (Fig. 30c–l, 37a, b, Table 16). Body highly fragile (especially the tail) and flexible, but acontractile. Trunk flattened up to 2:1 dorsoventrally, asymmetrical, that is, left margin straight to slightly convex, right distinctly convex; body narrowed in posterior quarter, producing conspicuous tail. Macronuclear nodules in middle third of trunk and, as is usual, slightly left of midline; individual nodules ellipsoidal (length:width ratio 2:1) to elongate ellipsoidal (4:1), contain numerous globular chromatin bodies. Micronuclei near or attached to macronuclear nodules, about 3 × 2 µm in life. Contractile vacuole behind buccal vertex. Cortical granules recognisable neither in life nor in protargol and

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cirrus at anterior end of paroral composed of 7–12, usually 9 kinetids. Adoral zone of membranelles about one third of body length, composed of 19 membranelles on average.

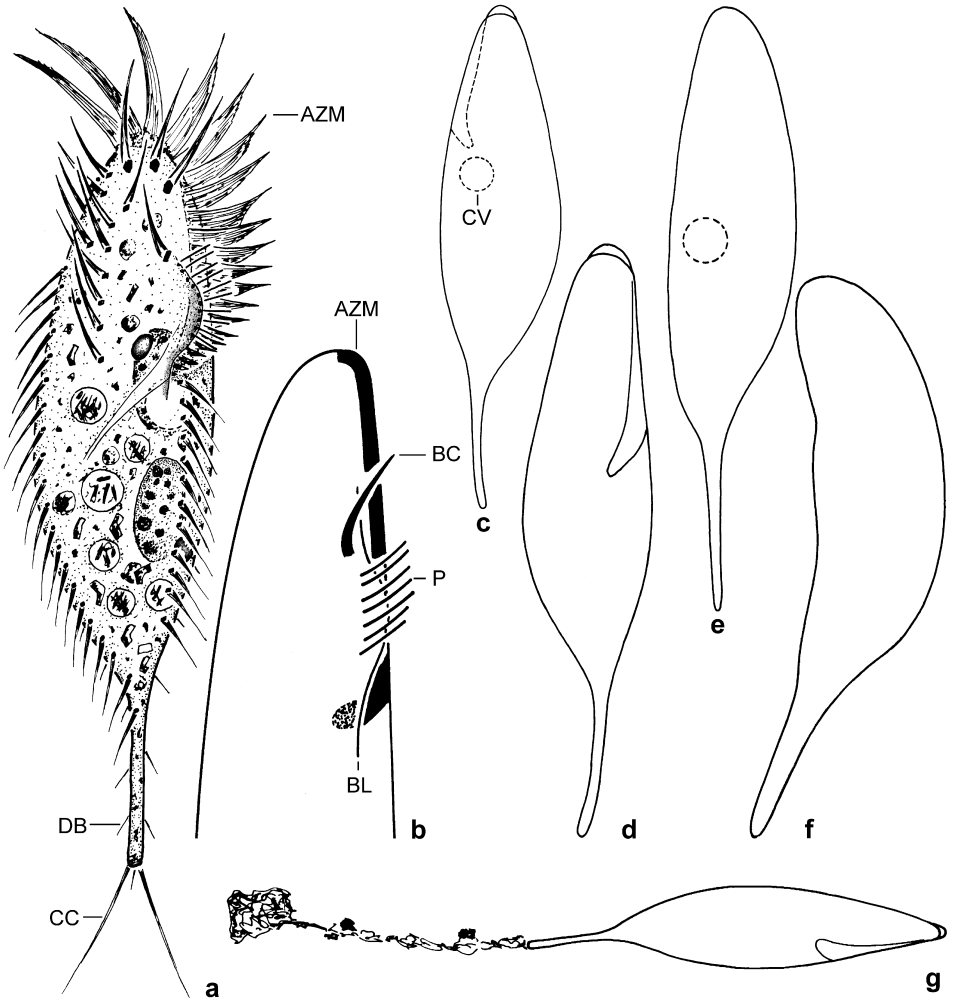


Fig. 30a–g *Paragonostomum (Paragonostomum) caudatum* (from Foissner et al. 2002a. From life. a, c, g, Australian population; b, f, Saudi Arabian specimens; d, e, Corsican specimens). **a:** Ventral view of a representative specimen, 76 µm. **b:** Anterior body portion at higher magnification. Note the conspicuous buccal lip covering the buccal cavity and the posterior portion of the adoral zone of membranelles. Furthermore, the lip carries the paroral. **c–f:** Dorsal (c, e, f) and ventral (d) views of shape variants. **g:** Specimen dragging a thread of mucous material recognisable by adhering debris. AZM = adoral zone of membranelles, BC = buccal cirrus, BL = buccal lip, CC = caudal cirri, CV = contractile vacuole, DB = dorsal bristle, P = paroral. Page 176.

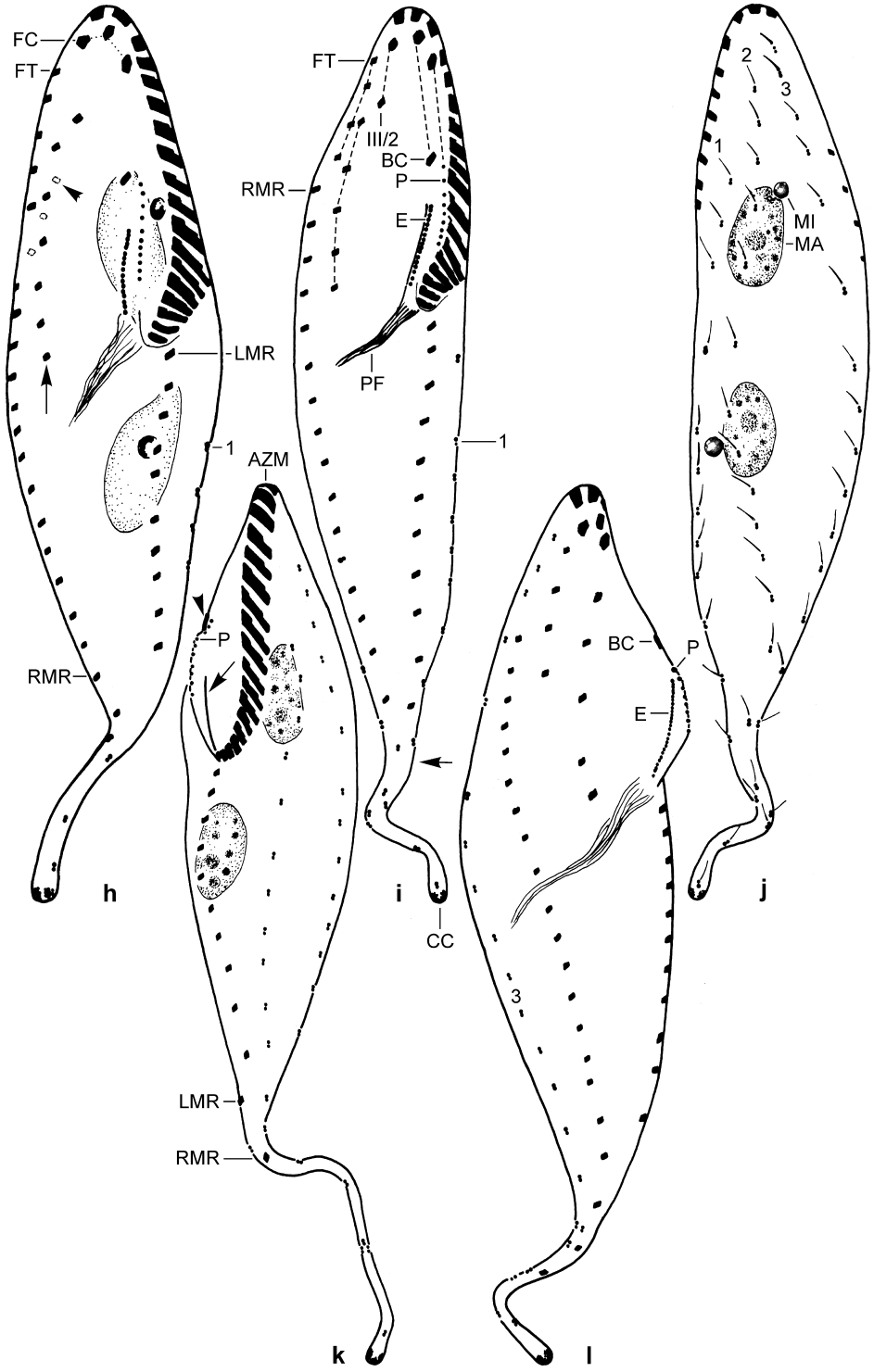
methyl green-pyronin preparations (Saudi Arabian population). Cytoplasm colourless, with few, about 3 µm-sized crystals and some lipid droplets 1–4 µm across. Glides rather rapidly on microscope slide, often motionless for some time; tail occasionally adheres to soil particles with a slimy thread (Fig. 30g).

Oral apparatus in *Gonostomum*-pattern (Fig. 30a, b, h, i, k, l; for detailed explanation, see Berger 1999, p. 56, 62). Adoral zone occupies about 44% of trunk length, but only about one third of body length, commences near midline of anterior body end and extends straight along left body margin, performing abrupt right bend to plunge into buccal cavity near left body margin; zone composed of an average of 19 membranelles, bases of largest membranelles about 4 µm wide. Proximal portion of adoral zone and buccal cavity partially covered by a curved, rather prominent cortical process (buccal lip) bearing the paroral, which is composed of 7–12 widely spaced, at least 5 µm long cilia. Buccal cavity narrow and flat, at right bordered by slightly curved endoral composed of tightly spaced basal bodies. Pharyngeal fibres clearly recognisable in life and after protargol impregnation, extend obliquely backwards.

Cirral pattern very constant, number of cirri of usual variability (Fig. 30h, i, k, l, Table 16). About 14 cirri on average on frontal area (all cirri included, except right marginal row). Frontal cirri about 13 µm long, moderately enlarged, arranged in typical *Gonostomum*-pattern, that is, left cirrus distinctly displaced posteriad (however, in contrast to the *Gonostomum*-pattern, cirrus I/1 is not distinctly greater than the other frontal cirri). Buccal cirrus slightly right and ahead of paroral. Frontoventral row usually slightly shorter, occasionally as long as adoral zone of membranelles, right of midline, with anteriormost cirrus (= cirrus III/2) shifted slightly to left (Fig. 30i) and thus behind right frontal cirrus. 4–5 frontoterminal cirri near or on right dorsolateral surface, form short row. Transverse cirri and pretransverse ventral cirri absent. Marginal cirri about 8 µm long in life; right row extends onto dorsal side anteriorly and usually terminates at base of tail; left row distinctly shortened posteriorly, that is, usually terminates ahead of base of tail.

Dorsal bristles about 3 µm long in life, arranged in three kineties, of which two or all extend onto tail (Fig. 30j, k). Kinety 1 commences near level of buccal cirrus and extends along left cell margin; kinety 2 extends slightly left of midline from near anterior body end to posterior trunk end; kinety 3 commences subapically and extends along right cell margin. Two or three (caudal?) cirri at top of tail, conspicuous in life because about 20 µm long and usually widely spread (Fig. 30a). Arrangement and composition of tail ciliature difficult to analyse because the tail is only 1.0–2.5 µm wide (see remarks in genus section).

Some additional data from the Turkish population described by Çapar (2007b; Fig. 31a–c): Body size 100–150 × 14–20 µm; body length:width ratio 5:1. Body outline clavate to lanceolate, cylindrical tail occupying about 17–20% of body length; left margin more or less straight, right distinctly convex. Macronuclear nodules 12–14 × 5–6 µm, in central portion of cell slightly left of midline. Cytoplasm colourless and with 1–4 µm-sized lipid droplets (Fig. 31a). Adoral zone occupies 35–40% of body length; proximal portion of adoral zone and buccal cavity partially covered by buccal lip. Paroral (not buccal lip as indicated by Çapar 2007b) composed of 7–12, about 6–7 µm long cilia. Three frontal cirri; one buccal cirrus; six or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seven frontoventral cirri; four or five frontoterminal cirri; three dorsal kineties; three caudal cirri (Fig. 31a–c).

Occurrence and ecology: Very likely confined to terrestrial habitats. The type locality of *Paragonostomum caudatum* is the Botanical garden of the town of Darwin (12°26'S 130°50'E), Australia, where it was discovered in the loamy soil of a meadow with some shrubs and trees (pH 7.1; Foissner et al. 2002a). In addition, we found *P. caudatum* in fine, blackish soil (pH 5.3) from the bank of the Rizzanes River near the town of Propriano, Corsica (collected by B. Ganner, Austria; September 1985); in a soil sample from the USA; in mouldy, about 10 cm thick, sandy *Casuarina*-litter (pH 7.2) on a dam near the village of Safwa, Saudi Arabia; and at several sites in Namibia (Foissner et al. 2002a). Further reliable records: blackish compost soil in a municipal compost plant of Munich, Germany (Foissner 2000, p. 259); soil of the inundation area of the Gelingüllü Dam lake (35°03'20"E 39°36'30"N), Yozgat Province, Turkey (Çapar 2007a, b); sandy soils from three sites in the surroundings of Riyadh, Saudi Arabia (Foissner et al. 2008a, p. 320). This wide distribution indicates that *P. caudatum* is a common and very likely cosmopolitan species preferring fine-grained mineral soils (Foissner et al. 2002a). *Paragonostomum caudatum* feeds on bacteria digested in vacuoles 4–5 µm across (Foissner et al. 2002a).

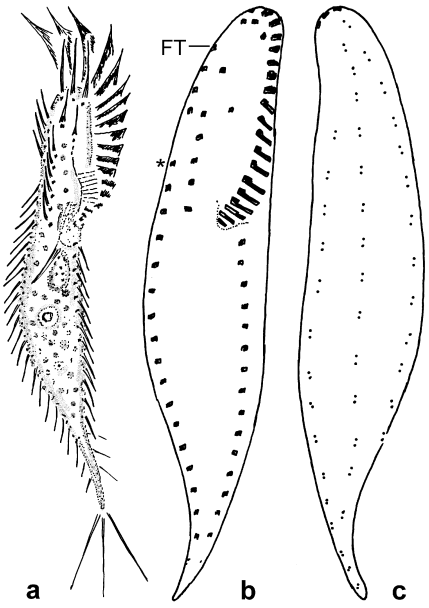

Fig. 31a–c *Paragonostomum (Paragonostomum) caudatum* (after Çapar 2007b. a, from life; b, c, protargol impregnation). **a:** Ventral view, 100–150 µm. **b, c:** Infraciliature of ventral and dorsal side (scale bar illustrated likely incorrect). Asterisk marks anterior end of right marginal row. FT = frontoterminal cirri. Page 176.

← **Fig. 30h–l** *Paragonostomum (Paragonostomum) caudatum* (from Foissner et al. 2002a. Protargol impregnation). **h:** Ventral side of a specimen (75 µm) with five frontoterminal cirri and six cirri in the frontoventral row (arrow marks rearmost cirrus of frontoventral row; cirrus III/2 not included). Arrowhead marks anterior end of right marginal row, which commences on dorsal side. Dotted line connects frontal cirri. **i, j:** Infraciliature of ventral and dorsal side of holotype specimen, 87 µm. Arrow in (i) denotes base of tail, as mentioned in Table 16. Broken lines connect cirri which very likely have been formed from the same anlage. If this assumption is correct, then one anlage (V?) is very likely lacking; however, this assumption has to be confirmed by morphogenetic data. **k:** Left side of a specimen with long tail. Arrow marks endoral membrane, arrowhead denotes buccal cirrus. **l:** Ventrolateral view showing the prominent buccal lip bearing the paroral (cp. Fig. 30b). AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri, E = endoral, FC = frontal cirri, FT = frontoterminal cirri, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = right marginal row, III/2 = cirrus behind right frontal cirrus, 1–3 = dorsal kineties. Page 176.

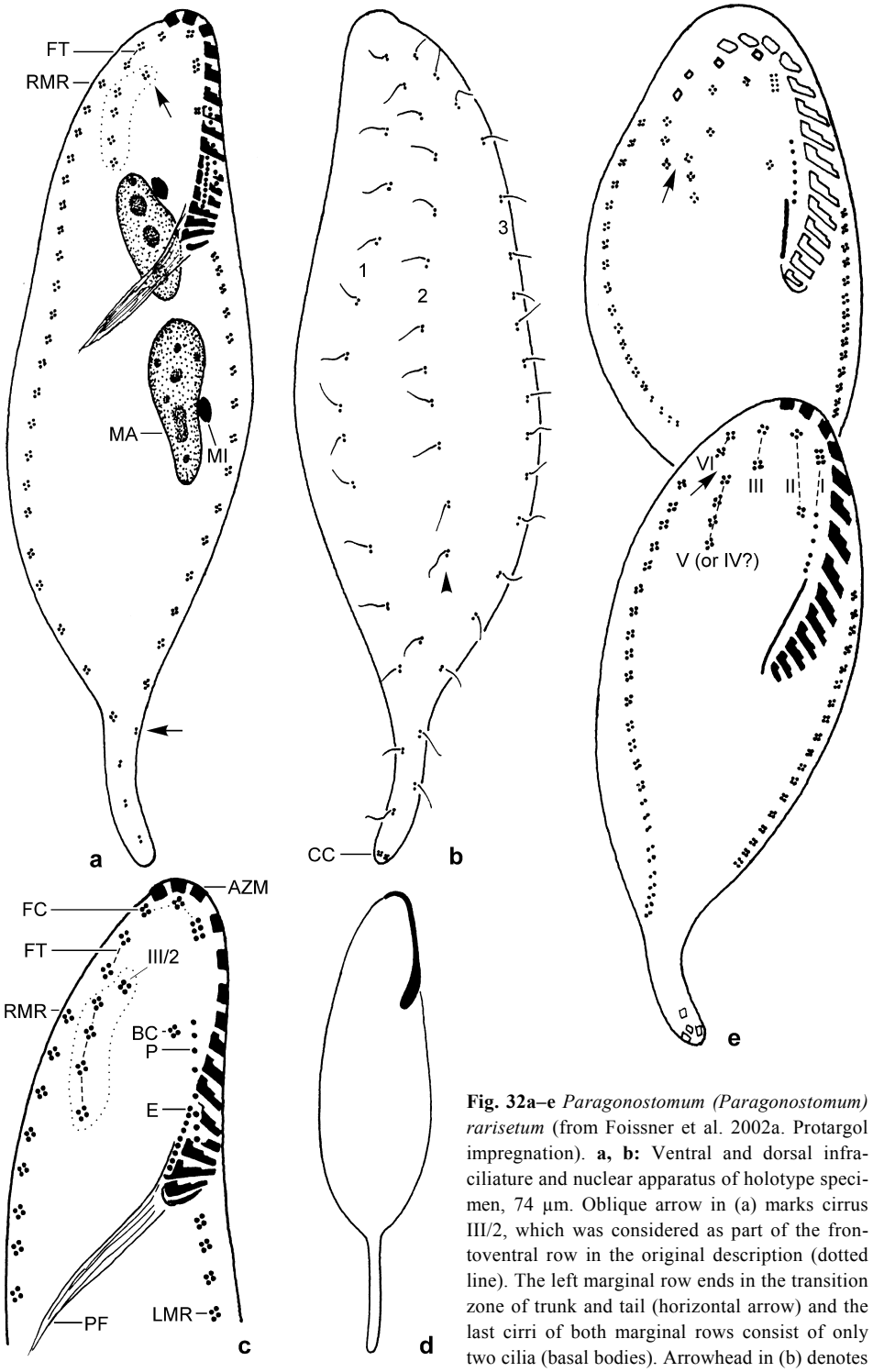

Fig. 32a–e *Paragonostomum (Paragonostomum) rarisetum* (from Foissner et al. 2002a. Protargol impregnation). **a, b:** Ventral and dorsal infraciliature and nuclear apparatus of holotype specimen, 74 µm. Oblique arrow in (a) marks cirrus III/2, which was considered as part of the frontoventral row in the original description (dotted line). The left marginal row ends in the transition zone of trunk and tail (horizontal arrow) and the last cirri of both marginal rows consist of only two cilia (basal bodies). Arrowhead in (b) denotes

Paragonostomum (Paragonostomum) rarisetum Foissner, Agatha & Berger, 2002 stat. nov.

(Fig. 32a–e, Table 16)

2002 ***Paragonostomum rarisetum* nov. spec.**[1] – Foissner, Agatha & Berger, Denisia, 5: 831, Fig. 181a–e, Table 159 (Fig. 32a–e; original description; one holotype slide [accession number 2002/429] and four paratype slides [2002/415, 430–432] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria, Foissner et al. 2002a, p. 41; Aescht 2008, p. 175).

Nomenclature: The species-group name *rarisetum* is a composite of the Latin quantifier *rarus* (few) and the Latin noun *saeta* (bristle, cirrus in present case), referring to the reduced number of frontoventral cirri (Foissner et al. 2002a).

Remarks: In life, the present species was identified as *P. caudatum* by Foissner et al. (2002a). From this species it is indistinguishable in size, shape, and general appearance. However, protargol impregnation revealed several distinct features, suggesting species status (Foissner et al. 2002a). We provided no detailed description, but a detailed comparison with related species.

Morphology: For a general morphology of the live specimens, see *P. caudatum* from which it is inseparable in this respect.

Paragonostomum rarisetum seemingly lacks frontoterminal cirri, that is, has only a single frontoventral row extending slightly obliquely from the distal end of the adoral zone to the mid of the frontal field (Fig. 32a, e). However, a late divider showed that two or three frontoterminal cirri are present which align ahead the row formed by the cirri of anlage V (or IV?). In other *Paragonostomum* species these cirral groups form two separate rows in interphasic specimens. In addition, the frontoventral row of *P. rarisetum*, although containing the frontoterminal cirri, is dis-

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← rear end of kinety 2. **c:** Infraciliature of anterior body portion in ventral view, 32 µm. Frontal cirri connected by dotted line; frontoventral row circled by dotted line. Note that the frontoterminal cirri and the cirri of anlage V (or IV?) form a continuous row which is reminiscent of the median cirral row of the amphisiellids (see Fig. 32e), a distinct difference to *P. caudatum*. The paroral is more or less continuous, a main difference between *P. (Paragonostomum)* and *P. (Bigonostomum)*. **d:** Shape variant, 84 µm. **e:** Late divider showing that the frontoventral row is formed by alignment (arrows) of the frontoterminal cirri (anlage VI) and the cirri of anlage V (or IV?). Cirri originating from same anlage connected by broken line. Note that no transverse cirri are formed. Parental structures white, new dotted or black. The loss of one frontoventral cirri anlage (IV or V) likely occurs in all *Paragonostomum* species except for *P. simplex* (see there). AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri, E = endoral, FC = frontal cirri, FT = frontoterminal cirri, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = anterior end of right marginal row, I–VI = frontalventral cirri anlagen, III/2 = cirrus behind right frontal cirrus, 1–3 = dorsal kineties. Page 183.

[1] Foissner et al. (2002a) provided the following diagnosis: Size about 85 × 20 µm in vivo. Lanceolate with conspicuous tail occupying about 25% of body length. 2 macronuclear nodules. On average 21 right marginal and 15 left marginal cirri; frontoventral and frontoterminal cirri form single row composed of 6 cirri on average and ending at 20% of body length; 1 buccal cirrus at anterior end of paroral composed of 6–9, usually 7 kinetids. Adoral zone of membranelles about 27% of body length, composed of 15 membranelles on average.

tinctly shorter than that of *P. caudatum* (extending 15 µm vs. 25 µm back from anterior body end; Table 16). Since the row consists of six cirri in both species, the cirri are obviously more closely spaced and the row commences more anteriorly in *P. rarisetum* than in *P. caudatum*. In total *P. caudatum* has 10 frontoventral and frontoterminal cirri, while *P. rarisetum* has only six on average, similar to *P. multinucleatum*.

The adoral zone of *P. rarisetum* is composed of 15 membranelles, while that of *P. caudatum* is made of 19. Accordingly, the adoral zone is shorter in *P. rarisetum* than in *P. caudatum*: 36% vs. 44% of trunk length; ratio of total body length:length of adoral zone 3.6:1 vs. 2.9:1 (Table 16).

Further observations from protargol preparations: macronuclear nodules obliquely arranged (Fig. 32a). Two or three cirri, each composed of two long cilia, at peak of tail; these cirri must be caudal cirri because no transverse cirri are recognisable in the late divider (Fig. 32e). Cilia of paroral about 10 µm long and loosely spaced, occasionally with an indistinct gap. Dorsal bristles 3–5 µm long.

Occurrence and ecology: Very likely confined to terrestrial habitats. Type locality of *Paragonostomum rarisetum* is the soil of an *Aloe dichotoma* forest near the Gariganus Guest farm (26°30'S 18°25'E; site 5 in Foissner et al. 2002a), Namibia. In total we found it at four sites, all in the Namib Escarpment, indicating that it prefers hot and dry conditions. We cannot exclude having mixed *P. rarisetum* with *P. caudatum* when live identifications were not checked in protargol preparations (Foissner et al. 2002a).

Paragonostomum (Bigonostomum) subgen. nov.

Nomenclature: The subgenus-group name *Bigonostomum* is a composite of the Latin numeral *bi-* (two) and *Gonostomum* (see *Gonostomum* for derivation) and refers to the bipartite paroral. Like *Gonostomum*, neuter gender. When somebody raises *Paragonostomum (Bigonostomum)* to genus rank, then the two species included have to be newly combined (ICZN 1999, Article 51.3.2).

Characterisation (A = supposed apomorphy): *Paragonostomum* with distinctly bipartite paroral (A). Frontoventral row usually composed of three cirri only (cirrus III/2 included; frontoterminal cirri not included).

Type species: *Paragonostomum multinucleatum* Foissner, Agatha & Berger, 2002a.

Remarks: For a foundation of the subgenus, see same chapter at genus section.

Species included in *Paragonostomum (Bigonostomum)* (alphabetically arranged basionyms are given): (1) *Paragonostomum binucleatum* Foissner, Agatha & Berger, 2002a; (2) *Paragonostomum multinucleatum* Foissner, Agatha & Berger, 2002a.

Key to *Paragonostomum (Bigonostomum)* species

1 Macronucleus composed of two nodules (Fig. 35a, e, g). . . . . *Paragonostomum (Bigonostomum) binucleatum* (p. 192)

- Macronucleus composed of seven nodules on average (Fig. 33a, d–f, i, j). . . . . *Paragonostomum (Bigonostomum) multinucleatum* (p. 185)

Paragonostomum (Bigonostomum) multinucleatum Foissner, Agatha & Berger, 2002 stat. nov.

(Fig. 33a–k, 34a–j, Table 16)

2002 ***Paragonostomum multinucleatum* nov. spec.**[1] – Foissner, Agatha & Berger, Denisia, 5: 828, Fig. 180a–k, Table 158 (Fig. 33a–k; original description; one holotype slide [accession number 2002/274], one paratype slide [2002/276], and four voucher slides [2002/277–280] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Foissner et al. 2002a, p. 41; Aescht 2008, p. 167).

2006 ***Paragonostomum multinucleatum* Foissner, Agatha et Berger, 2002** – Vdačny & Tirjaková, Biologia, Bratislava, 61: 513, Fig. 6A–J, Table 2 (Fig. 34a–j; detailed description of Slovakian population).

Nomenclature: The species-group name *multinucleatus*, *-a*, *-um* (Latin adjective [m, f, n]; having many nuclei) is a composite of the Latin quantifier *mult-* (many), the thematic vowel *-i-*, and *nucleatum* (having a nucleus), and refers to the increased number of macronuclear nodules, a main feature of this species (Foissner et al. 2002a). Type species of *Paragonostomum (Bigonostomum)*. Paratype (accession number 2002/276) lost as indicated by W. Foissner on an external sheet of paper (details see Aescht 2008, p. 167).

Remarks: *Paragonostomum multinucleatum* differs from most other *Paragonostomum* species and *Gonostomum namibiense*, inter alia, by the number of macronuclear nodules (4–9 vs. 2). *Paragonostomum simplex* also has more than two macronuclear nodules (8–15), but differs from *P. multinucleatum* in body shape (tail lacking vs. present), the higher number of cirri on frontal area, the position of the buccal cirrus (distinctly ahead of paroral against close to anterior end), and the paroral (continuous vs. bipartite).

Vdačny & Tirjaková (2006) found distinct differences between the Slovakian population and the populations described by Foissner et al. (2002a), namely, in the number of kinetids in dorsal kinety 2, the length of the paroral, and the number of

[1] Foissner et al. (2002a) provided the following diagnosis: Size about 75 × 15 µm in vivo. Pisciform with tail-like posterior portion occupying about 20% of body length. On average 7 macronuclear nodules forming distinct strand, 22 right marginal, 16 left marginal, 2 frontoterminal, and 3 frontoventral cirri; 1 buccal cirrus in front of paroral composed of 4–7, usually 6 kinetids divided into an anterior and posterior segment by a small gap. Adoral zone of membranelles about one third of body length, composed of 19 membranelles on average.

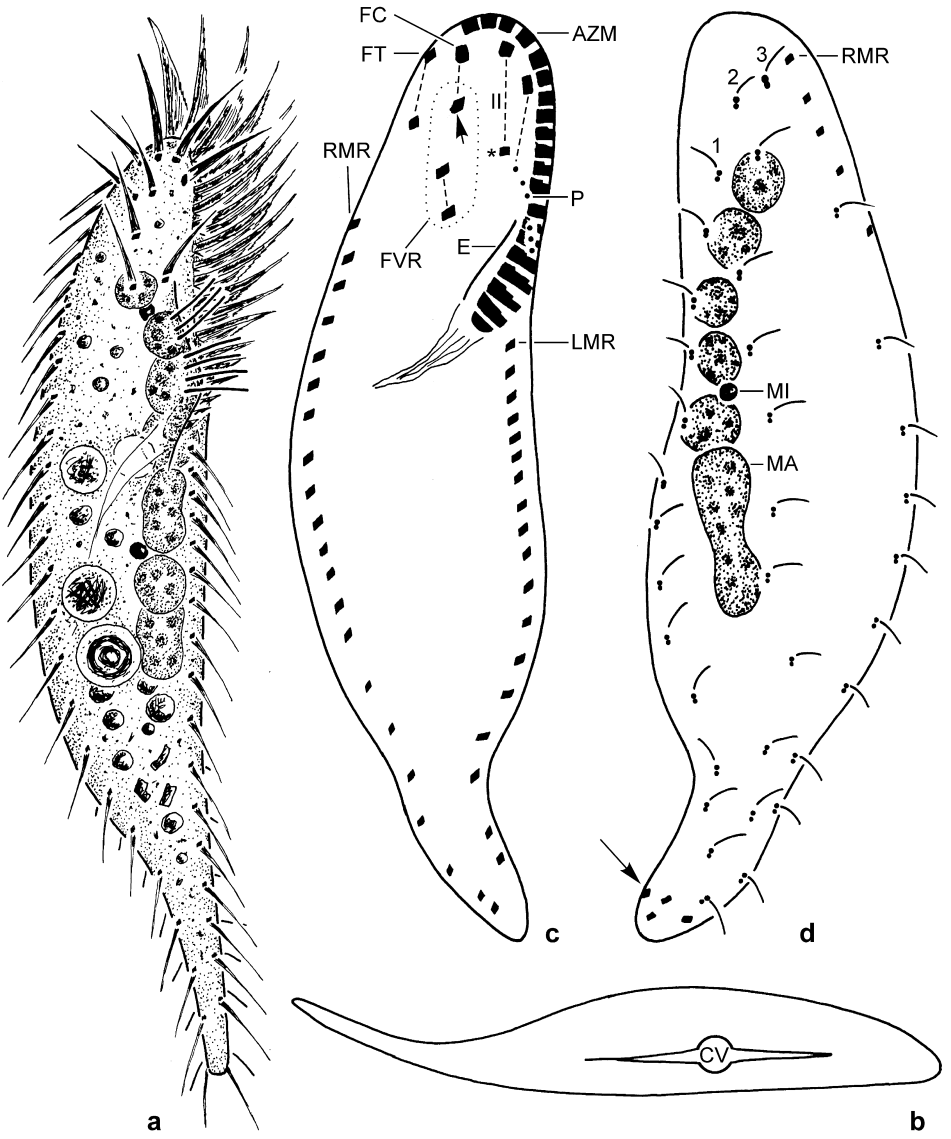


Fig. 33a–d *Paragonostomum (Bigonostomum) multinucleatum* (from Foissner et al. 2002a. a, b, from life; c, d, protargol impregnation. a–d, type population). **a:** Ventral view of a representative specimen, 73 µm. **b:** Ventral view of pisciform specimen showing location of contractile vacuole with collecting canals. **c, d:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 63 µm. Short arrow in (c) marks cirrus III/2, asterisk denotes buccal cirrus. Frontal cirri connected by dotted line; frontoventral row encircled by dotted line. Broken line connects cirri which very likely are formed by the same anlage (has to be confirmed by ontogenetic data). Arrow in (d) marks cirri at top of tail, which is rather distorted and possibly turned up side down so that marginal cirri give the impression of caudal cirri. AZM = adoral zone of membranelles, CV = contractile vacuole, E = endoral, FC = frontal cirri, FT = frontoterminal cirri, FVR = frontoventral row (a pseudorow because composed of cirri of two different anlagen), LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = right marginal row, II = frontal-ventral anlage II (forms middle frontal cirrus and buccal cirrus), 1–3 = dorsal kineties. Page 185.

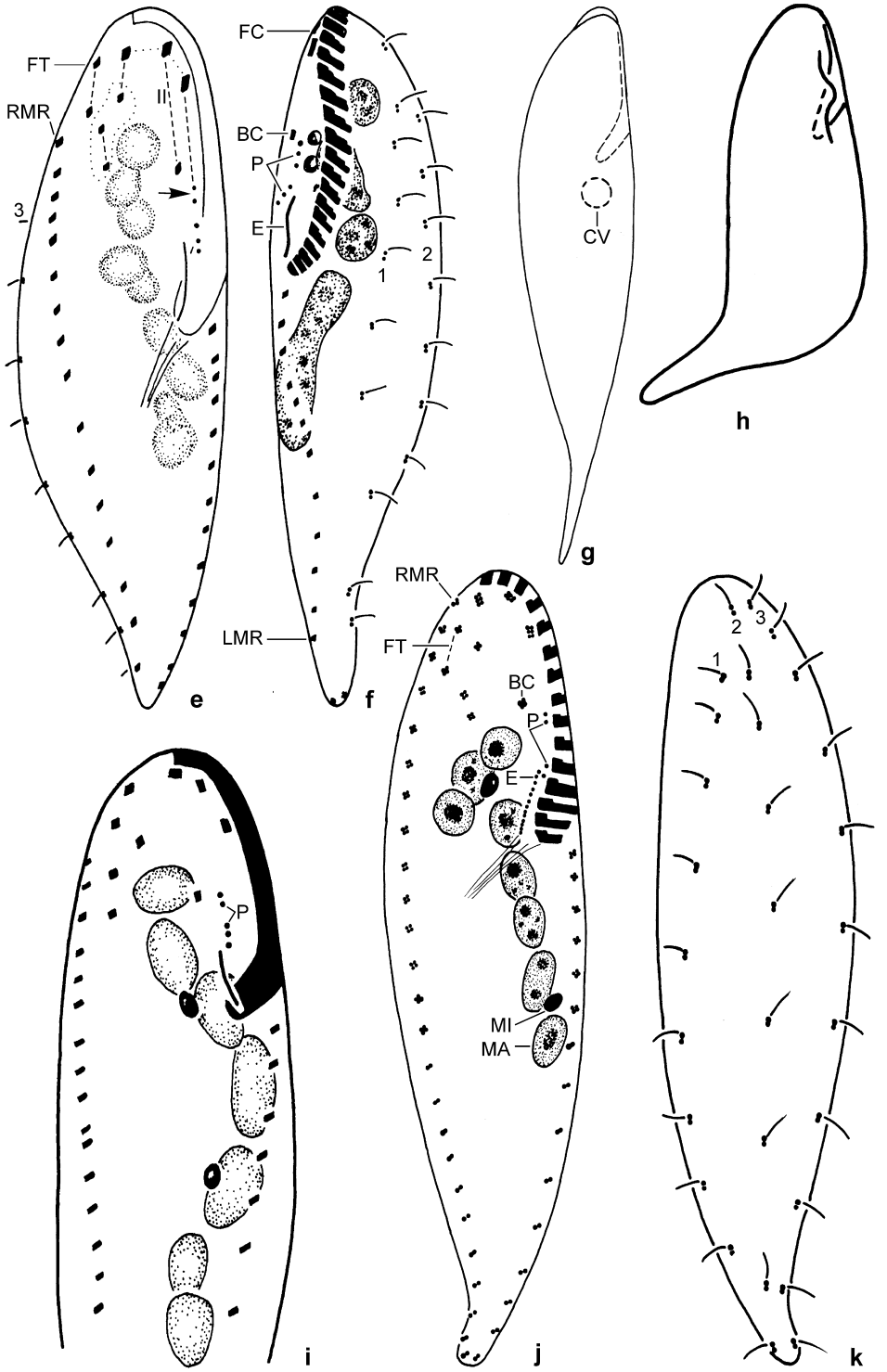
paroral cilia (details see Table 16). Further populations have to be studied to estimate the meaning of these differences.

Morphology: We studied two populations (Foissner et al. 2002a). The specimens from the USA-population (Fig. 33g–k, Table 16) match those from the type population (Fig. 33a–f) very well, both in morphology and morphometrics, so that conspecificity is beyond reasonable doubt. For a characterisation of the Slovakian population, see Fig. 34a–j and Table 16.

Body size 60–90 × 13–25 µm in life, usually about 75 × 15 µm, length:width ratio 3.0–4.5:1, on average 3.8:1 in protargol preparations, where specimens are more or less inflated since they are rather fragile (Table 16). Body elongate and tail-like narrowed posteriorly in live and protargol preparations; only slightly flattened and asymmetrical, left margin straight to slightly sigmoidal, right slightly to distinctly convex and narrowed in posterior quarter producing tail-like elongation; acontractile, but very flexible (Fig. 33a–c). Macronuclear nodules mainly left of midline in series, sometimes in C-shaped pattern, some nodules occasionally separated by small gaps; individual nodules globular to ellipsoidal (2:1), rarely dumb-bell-shaped or elongate ellipsoidal indicating that two or three nodules have not separated, contain globular chromatin bodies. Micronuclei near or attached to macronuclear nodules, globular, inconspicuous because tiny and rather hyaline. Contractile vacuole right of buccal vertex, that is, in or near body midline; during diastole with two collecting canals (Fig. 33b). Cortical granules obviously lacking because recognisable neither in life nor in protargol preparations. Cytoplasm colourless, with few, about 2–3 µm-sized crystals and some lipid droplets 1–3 µm across in posterior body portion. Glides rather rapidly on microscope slide.

Oral apparatus in *Gonostomum* pattern (details see Berger 1999). Adoral zone occupies only slightly more than one third of body length, commences near midline of anterior body end and extends straight along left body margin, performing abrupt bend to plunge into buccal cavity near left body margin; composed of an average of 19 membranelles, bases of largest membranelles about 4 µm wide. Proximal portion of adoral zone and buccal cavity almost entirely covered by a curved, rather prominent buccal lip bearing the paroral. Paroral as in *P. binucleatum*, that is, divided into an anterior segment with 1–3 and a posterior segment with 2–4 widely spaced, about 8 µm long cilia (Fig. 33a, c, e, f, i, j). Buccal cavity very narrow and flat, at right bordered by slightly curved endoral composed of tightly spaced basal bodies. Pharyngeal fibres clearly recognisable in life and after protargol impregnation, extend obliquely backwards.

Cirral pattern very constant, number of cirri of usual variability (Fig. 33c–f, i, j; Table 16). Nine cirri on average on frontal area, namely three moderately enlarged frontal cirri about 10 µm long and in typical *Gonostomum*-pattern, that is, left one displaced posteriad (but not distinctly larger than the other two frontal cirri, as is the case with *Gonostomum*); one buccal cirrus right and ahead of anterior end of paroral; one cirrus (III/2) behind right frontal cirrus; two cirri behind and slightly rightwards of cirrus III/2 (these two cirri and cirrus III/2 termed frontoventral row in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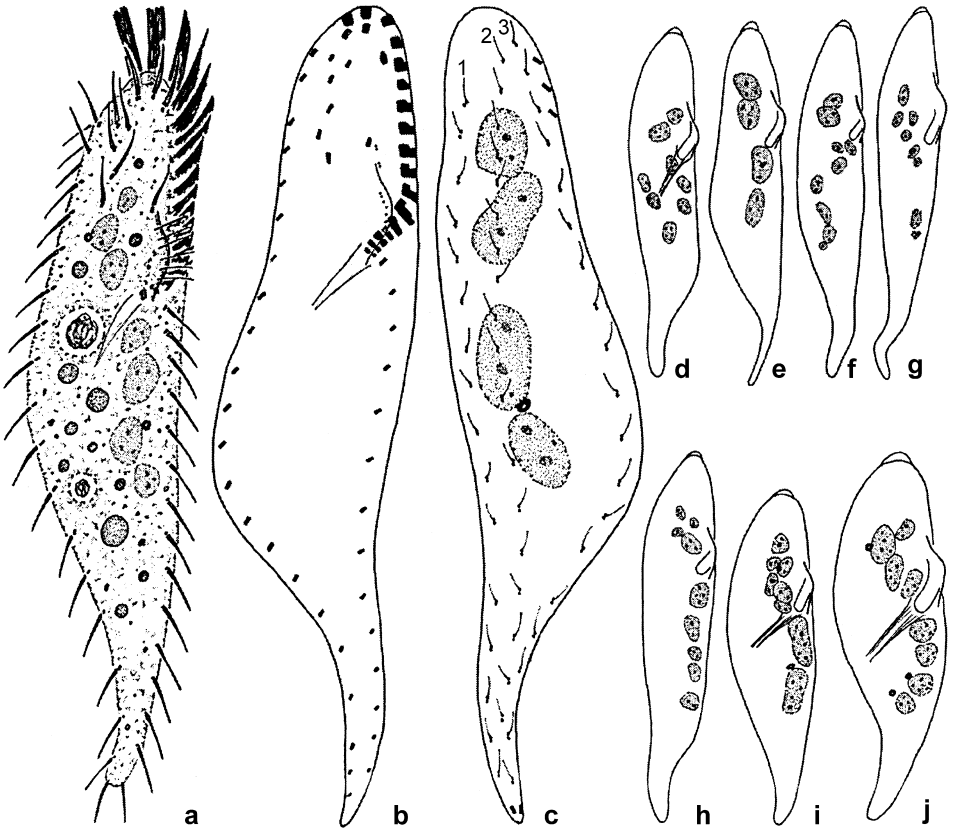
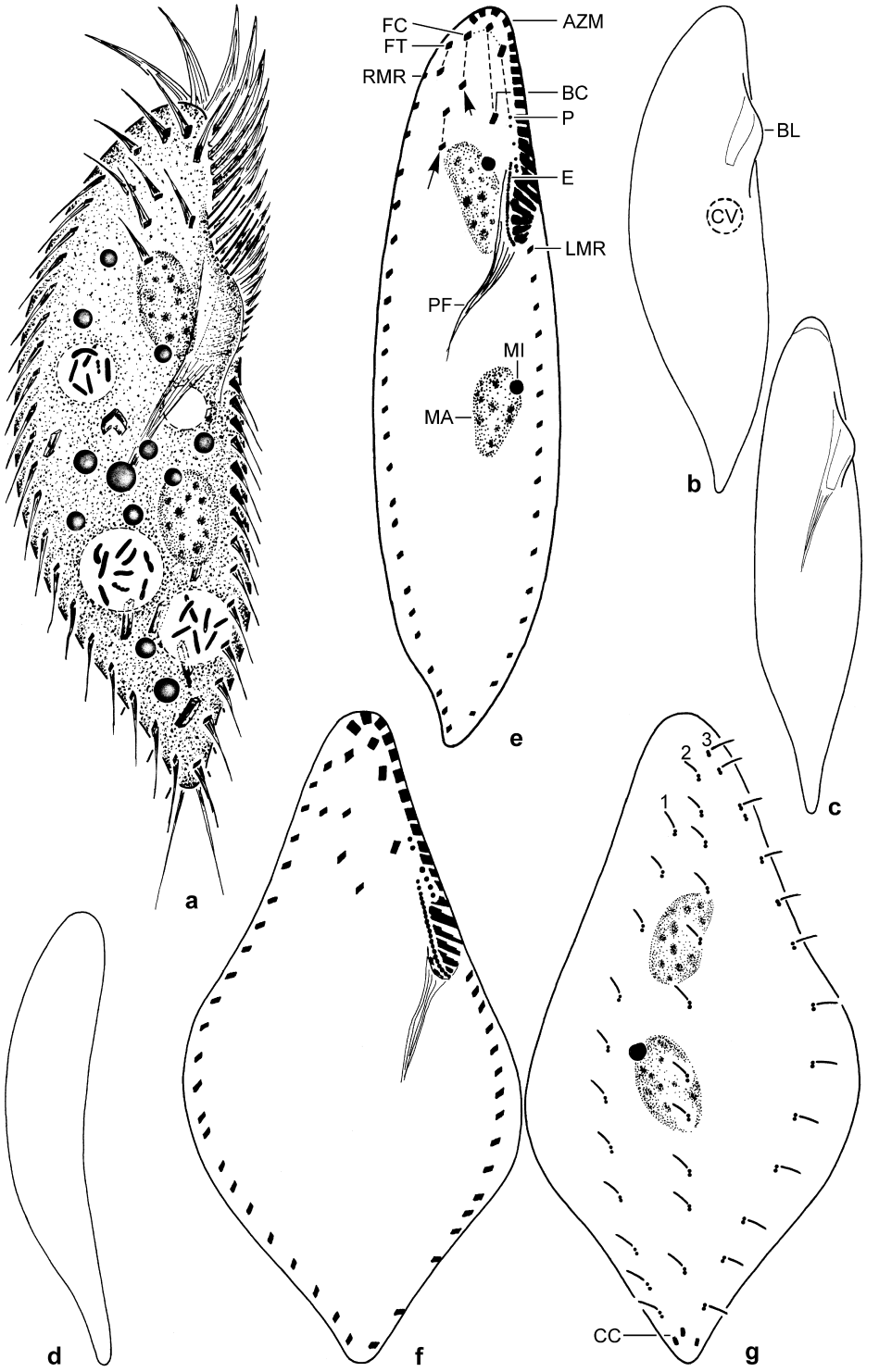


Fig. 34a–j *Paragonostomum (Bigonostomum) multinucleatum* (from Vdačny & Tirjaková 2006. a, from life; b–j, protargol impregnation). **a:** Ventral view, 60 µm. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 67 µm. Detailed labelling, see previous figures. **d–j:** Variability of body outline and nuclear apparatus. 1–3 = dorsal kineties. Page 185.

← **Fig. 33e–k** *Paragonostomum (Bigonostomum) multinucleatum* (from Foissner et al. 2002a. e, f, i–k, protargol impregnation; g, h, from life. e, f, type population; g–k, USA population). **e:** Infraciliature and nuclear apparatus of a specimen (56 µm) with two basal bodies in anterior segment of paroral (arrow). Frontal cirri connected by dotted line; frontoventral cirri circled by dotted line (cirrus III/2 included); cirri (very likely) originating from same anlage connected by broken line. **f:** Left lateral view of infraciliature and nuclear apparatus, 57 µm. **g:** Ventral outline of a representative specimen. **h:** Specimens slightly squeezed between slide and cover glass obtain a characteristic shape. **i:** Infraciliature of ventral side and nuclear apparatus of a specimen with the common paroral pattern, that is, the anterior and posterior segment are separated by the space of one cilium. **j, k:** Infraciliature of ventral and dorsal side and nuclear apparatus of a specimen (58 µm) with widely separated paroral segments. Note that the marginal cirri of the posterior body portion are composed of two basal bodies only; on the thin tail they are thus difficult to distinguish from the dorsal dikinetids. BC = buccal cirrus, CV = contractile vacuole, E = endoral, FC = frontal cirri, FT = frontoterminal cirri, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = bipartite paroral, RMR = right marginal row, II = frontal-ventral anlage II (forms middle frontal cirrus and buccal cirrus), 1–3 = dorsal kineties. Page 185.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original description); two frontoterminal cirri with anterior one almost at level of right frontal cirrus and on or near dorsolateral side; the arrangement indicates that one anlage (IV [or V?]) is lacking in this and most other *Paragonostomum* species. Transverse cirri absent. Marginal cirri about 7 µm long in life; right row commences on dorsal side of anterior end, terminates, like left row, near rear cell end; left row commences left of proximal end of adoral zone; posterior marginal cirri composed of two basal bodies only and thus very fine.

Dorsal bristles about 3 µm long in life, arranged in three more or less bipolar kineties (Fig. 33d). Details of pattern and presence/absence of caudal cirri difficult to analyse because of tailed body; in life, the cirri at the end of the tail are inconspicuous (Fig. 33a).

Occurrence and ecology: Very likely confined to terrestrial habitats. Type locality of *Paragonostomum multinucleatum* is a highly saline crust soil from small quartz stones about 1 km inshore of the Great Bay of the town of Lüderitz (26°40'S 15°10'E), Namibia (site 11 in Foissner et al. 2002a). Foissner et al. (2002a) described a second population which is also from an extreme habitat, namely, the Warm Sonoran Desert in Arizona, USA, where *P. multinucleatum* occurred in the litter and upper soil layer under *Ephedra* sp. ("marmon tea", jointed firs), a gymnospermous belonging to the Ginetophyta (collected by Stuart S. Bamforth on May 21, 1988 at 11h30, when soil temperature was 40°C under *Ephedra*). Vdačny & Tirjaková (2006) found *P. multinucleatum* in soil mixed with roots and little branches (collected on July 18, 2005) from the Cerová vrchovina highlands (48°10'N 19°54'E) in Slovakia. Recently, Foissner et al. (2008a, p. 320) found it in saline soil (21‰; pH 6.7) covered with halophilous vegetation, about 150 km northwest of Riyadh, Saudi Arabia. Likely, *Paragonostomum multinucleatum* is euryhaline and cosmopolitan. Feeds on bacteria and coccal green algae digested in vacuoles 4–6 µm across (Foissner et al. 2002a).

← **Fig. 35a–g** *Paragonostomum (Bigonostomum) binucleatum* (from Foissner et al. 2002a. a–d, from life; e–g, protargol impregnation). **a:** Ventral view of a representative specimen (76 µm) with outline redrawn from a micrograph of a freely motile cell. **b–d:** Shape variants in ventral (b, c) and right lateral (d) view showing location of contractile vacuole, buccal lip, and dorsoventral flattening. **e:** Infraciliature and nuclear apparatus of a slender, non-inflated specimen (83 µm) with, exceptionally, four dorsal kineties. Short arrow marks cirrus III/2, long arrow marks rear end of frontoventral row (= cirrus IV/2). The pattern strongly indicates that anlage V is lacking in this and the other *Paragonostomum* species (cp. with Fig. 36k). Broken lines connect cirri, which – very likely – originate from the same anlage. Dotted line connects frontal cirri. **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 75 µm. AZM = adoral zone of membranelles, BC = buccal cirrus, BL = buccal lip, CC = caudal cirri, CV = contractile vacuole, E = endoral, FC = frontal cirri, FT = frontoterminal cirri, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = right marginal row, 1–3 = dorsal kineties. Page 192.

Paragonostomum (Bigonostomum) binucleatum Foissner, Agatha & Berger, 2002 stat. nov.

(Fig. 35a–g, 37c, Table 16)

2002 ***Paragonostomum binucleatum* nov. spec.**[1] – Foissner, Agatha & Berger, Denisia, 5: 826, Fig. 179a–g, 381u, Table 158 (Fig. 35a–g, 37c; original description; one holotype slide [accession number 2002/602] and four paratype slides [2002/603–606] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Foissner et al. 2002a, p. 41; Aescht 2008, p. 146).

Nomenclature: The species-group name *binucleat·us*, *-a*, *-um* (Latin adjective [m; f; n]; having two nuclei) is a composite of the Latin numeral *bi-* (two) and *nucleatum* (having a nucleus) and refers to the two macronuclear nodules, a main feature of this species (Foissner et al. 2002a).

Remarks: Differs from *P. multinucleatum* only by the number of macronuclear nodules (2 vs. 4–13, usually 7). The tail is usually slightly longer in *P. multinucleatum* than in *P. binucleatum* (Fig. 33a, 35a–c, 37a–c). However, it is rather variable and thus should not be used as a distinguishing feature. Like the other *Paragonostomum* species, it is very fragile and thus usually more or less inflated and distorted in ordinary protargol preparations (Foissner et al. 2002a).

Paragonostomum rarisetum has a similar size and the same nuclear pattern (Fig. 32a). However, its tail is more distinct (25% of body length vs. 10%), the number of frontoventral and frontoterminal cirri is higher (7 vs. 5), and the number of adoral membranelles is lower (15 on average vs. 21). In addition, it has a continuous paroral (vs. bipartite).

Gonostomum namibiense Foissner, Agatha & Berger, 2002, which has a similar size and shape and the same nuclear pattern, has transverse cirri (Fig. 22a–j). In addition, it possesses cortical granules, which are, however, difficult to recognise because they are minute (1.0 × 0.3 µm) and colourless. *Gonostomum algicola* is also rather similar, but usually lacks a tail, has only four paroral kinetids in a short, continuous row, and possesses one transverse cirrus, which is, however, difficult to recognise. Thus reliable species identification requires protargol impregnation or very careful live observation (Foissner et al. 2002a).

Morphology: *Paragonostomum binucleatum* very closely resembles *P. multinucleatum* (previous species), except for the number of macronuclear nodules (2 vs. 7). Thus, we provided no description, but referred the reader to the description of *P. multinucleatum* and the detailed figures and morphometry of *P. binucleatum* (Fig. 35a–g, 37c, Table 16).

Occurrence and ecology: Likely confined to terrestrial habitats. Type locality of *P. binucleatum* is the village of Sharm el Sheik (27°N 34°E), Sinai, Egypt, where we

[1] Foissner et al. (2002a) provided the following diagnosis: Size about 70 × 23 µm in vivo. Pisciform with tail-like posterior portion occupying about 10% of body length. 2 macronuclear nodules. On average 21 right marginal, 15 left marginal, 2 frontoterminal, and 3 frontoventral cirri; 1 buccal cirrus at anterior end of paroral composed of 4–8, usually 6 kinetids divided into an anterior and posterior segment by a small gap. Adoral zone of membranelles about 37% of body length, composed of 21 membranelles on average.

discovered it in a lawn of a hotel with moderate abundance (Foissner et al. 2002a). The soil was very likely artificial (compost or composted activated sludge) because it was only an about 5 cm thick layer above the sandy ground. It was black and "fat", hardly containing any litter, had a pH of 8.2, and was sown with lawn grasses a few days before (Foissner et al. 2002a). Furthermore, *P. binucleatum* occurred in four Namibian sites (33, 49, 52, 56), where it was rare (detailed description of sites, see Foissner et al. 2002a, p. 15ff). Foissner et al. (2008a, p. 320) found it about 150 km northwest of Riyadh, in the surroundings of the village of A-Qasab (Al-Kasab) in a very sandy soil of a pasture land in a semi-desert.

Incertae sedis in *Paragonostomum*

Remarks: The two species reviewed below do not have a more or less distinct tail, a diagnostic feature of *Paragonostomum* according to the original description (Foissner et al. 2002a). However, they lack transverse cirri – also a main feature of *Paragonostomum* – so that their original assignment is preliminary retained. Because of the uncertainties I refrain from a subgeneric assignment. Interestingly, both species have cortical granules, organelles which are lacking in the tailed *Paragonostomum* species. Detailed morphological, ontogenetic, and molecular analyses are needed to get a better insight into the phylogenetic relationships of these species. The third non-tailed *Paragonostomum* species described so far (*P. ghangriai*) is transferred to *Neowallackia* (p. 280).

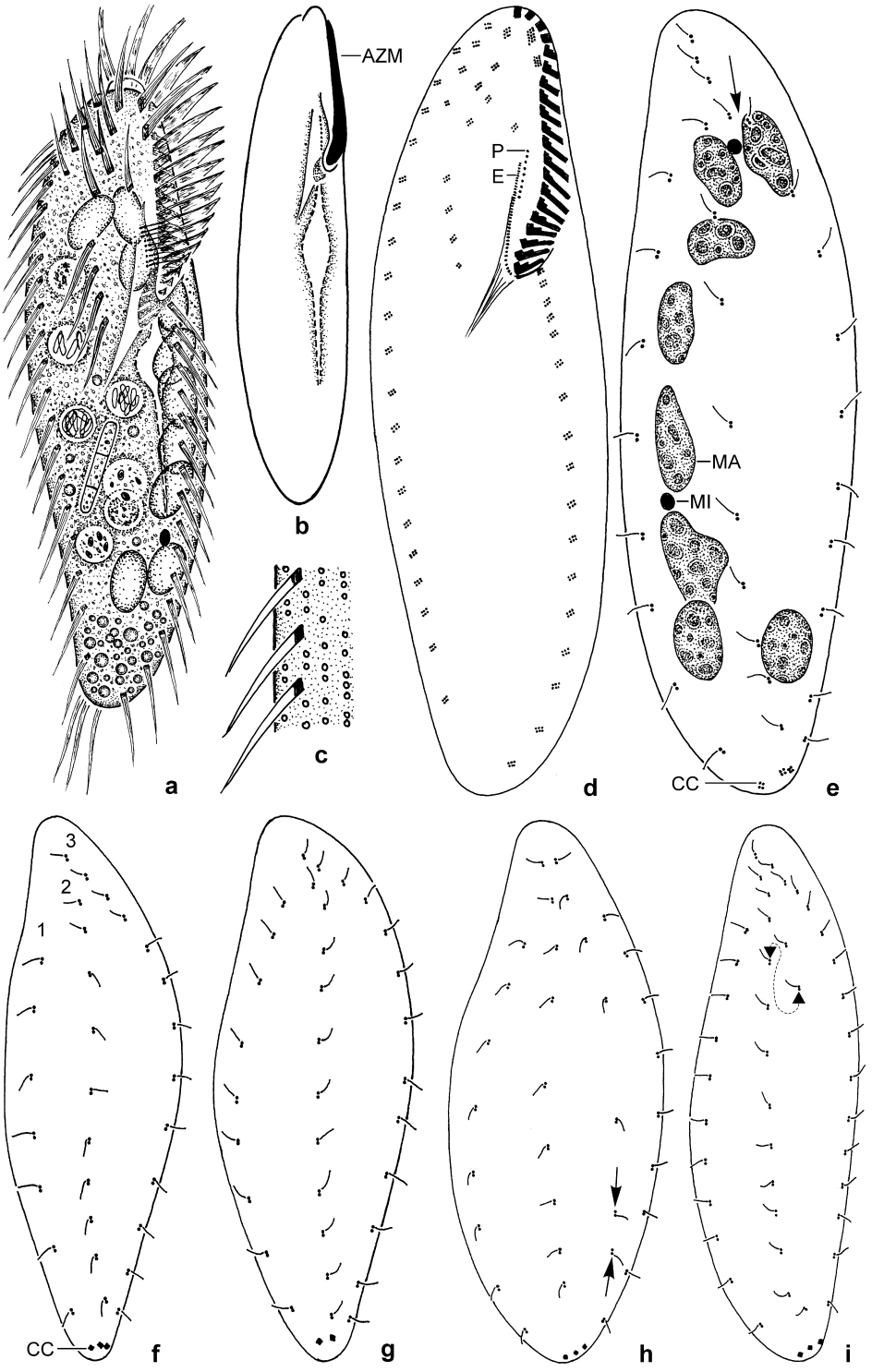
Paragonostomum simplex Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005

(Fig. 36a–j, 37d, e, Table 17)

2005 ***Paragonostomum simplex* nov. spec.**[1] – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiversity and Conservation, 14: 674, Fig. 13c, f, 14a–i, Table 10 (Fig. 36a–i, 37d, e; original description; according to Foissner et al. 2005, p. 674, one holotype slide and four paratype slides have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria [further details see nomenclature]).

Nomenclature: The species-group name *simplex* (Latin adjective; simple) refers to the fact that generic classification is easier than in the congeners, where the lack of the transverse cirri is difficult to prove due to the tailed posterior body end (Foissner et al. 2005).

[1] Foissner et al. (2005) provided the following diagnosis (only data from the type population have been included): Size about 85 µm × 25 µm in vivo; elongate to indistinctly sigmoidal with narrowly rounded posterior end. On average 10 macronuclear nodules in C-shaped pattern left of midline, 21 right marginal, 16 left marginal, 4 frontoterminal, 8 frontoventral, and 3 caudal cirri; 1 buccal cirrus far above paroral membrane composed of an average of 9 kinetids in continuous row. Adoral zone of membranelles occupies about 37% of body length, composed of 20 membranelles on average.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According to Aescht (2008, p. 178) one holotype slide (accession number 2007/681) and six paratype slides have been deposited in the museum in Linz. However, only five paratype slides (2007/678, 679, 680, 681, 682) – including the holotype slide (2007/681) – are mentioned in the review by Aescht, indicating that the original statement by Foissner et al. (2002a; one holotype and four paratype slides) is correct; of course, the holotype slide also contains paratype specimens.

Remarks: For a foundation of the classification as incertae sedis in *Paragonostomum*, see remarks at genus section.

Paragonostomum (Bigonostomum) multinucleatum, the sole congener with more than two macronuclear nodules, has a bipartite paroral, a distinctly tailed body, and less frontoventral cirri. In addition, the buccal cirrus is distinctly ahead of the paroral in *P. simplex*, whereas it is close to the anterior end in *P. multinucleatum* (Foissner et al. 2005).

The populations investigated differ in the presence/absence of cortical granules, an important difference usually used to characterise species. However, the granules are colourless and sometimes loosely arranged so that it cannot be excluded that we have overlooked them in the type population (Foissner et al. 2005).

In life, *Paragonostomum simplex* highly resembles *Gonostomum* species, especially *G. kuehnelti*, which also has many macronuclear nodules (p. 109). However, *Gonostomum* has transverse cirri, whereas this cirral group is unequivocally lacking in *P. simplex*.

Morphology: Three Austrian populations were studied by Foissner et al. (2005), namely from the Stampfltal (type locality), Merckenstein (a site near the type locality), and from a beech forest in Salzburg. The populations match very well, both in life and protargol preparations, showing that *P. simplex* is a well defined species. Thus, the description below contains data from all populations. The specimens from Merckenstein and Salzburg have more or less distinct cortical granules, likely overlooked in the type population (see remarks).

Body size about 70–110 × 20–30 µm in life, usually near 90 × 25 µm; body length:width ratio about 3.3–3.5:1 in life, while 3:1 in protargol preparations (Table 17), where specimens tend to become inflated in mid-body. Body outline slender with both ends narrowly rounded, never tailed, usually slightly fusiform and sigmoidal, right margin often more distinctly convex than left (Fig. 36a, b). Body dorsoventrally flattened up to 2:1; non-contractile. Macronuclear nodules arranged roughly

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← **Fig. 36a–i** *Paragonostomum simplex* (from Foissner et al. 2005. a–c, from life; d–i, protargol impregnation). **a:** Ventral view of a representative specimen, 83 µm. **b:** Outline, contractile vacuole with collecting canals, and scheme of oral apparatus of slender specimen. **c:** Surface showing cortical granulation of a specimen from Merckenstein. **d, e:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 82 µm. Arrow in (e) marks break in dorsal kinety 3. **f:** Typical specimen with three dorsal kineties and one caudal cirrus per kinety, 66 µm. **g:** Specimen with ordinary dorsal kineties but only two caudal cirri, 64 µm. **h:** Specimen with a fourth kinety between bristle rows 2 and 3, 79 µm. Arrows mark dikinetids with reversed polarity. **i:** Specimen with break in kinety 2 (double arrow), 83 µm. AZM = adoral zone of membranelles, CC = caudal cirri, E = endoral, MA = macronuclear nodule, MI = micronucleus, P = paroral, 1–3 = dorsal kineties. Page 193.

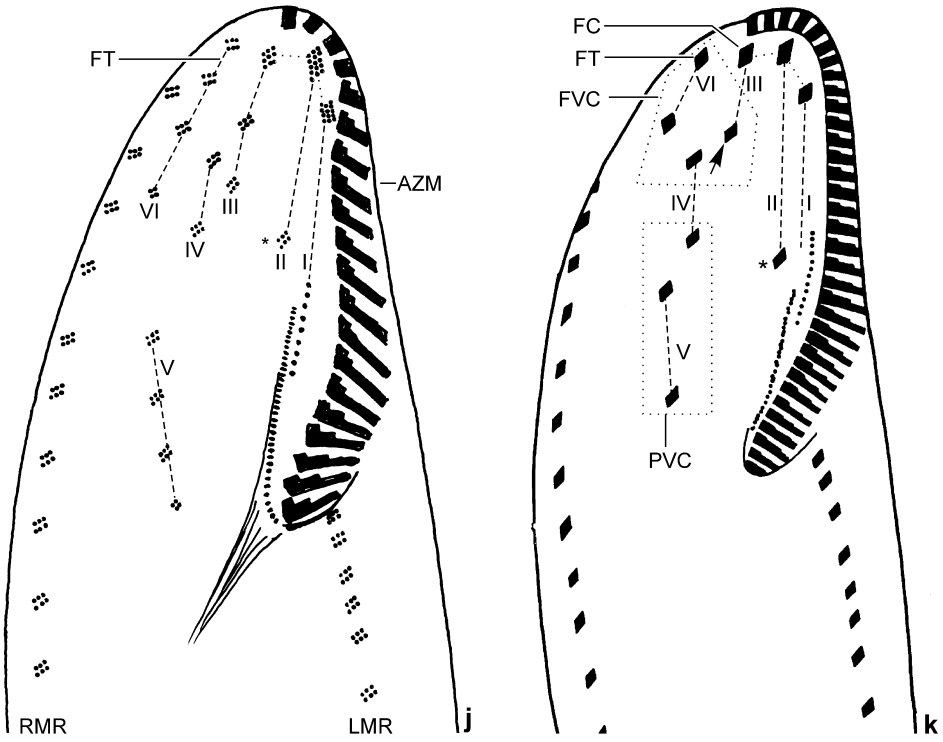

Fig. 36j *Paragonostomum simplex* (anterior portion of Fig. 36d, modified). Supposed origin of frontoventral cirri from anlagen I–VI (has to be confirmed by ontogenetic data). Note that *P. simplex* has – like *Gonostomum affine* (k) – the ordinary number of six frontal-ventral cirri anlagen, whereas the tailed *Paragonostomum* species and the two Indian species have (very likely) only five anlagen. Dotted line connects frontal cirri, broken lines connect cirri originating from same anlage. Asterisk marks buccal cirrus. Page 193.
Fig. 36k *Gonostomum affine* (from Berger & Foissner 1988, modified. Protargol impregnation). In *Gonostomum* the frontoventral cirri are formed from the ordinary number of six (I–VI) anlagen. *Gonostomum* is basically an 18-cirri hypotrich with the postoral ventral cirri (dotted rectangle) right of the proximal portion of the adoral zone. This illustration shall demonstrate the similarity between the cirral pattern of *Gonostomum* and *Paragonostomum* (see remarks at genus section of *Paragonostomum*). Unfortunately, one cannot decide unequivocally which of the two cirral pairs/anlagen (IV or V) is lacking in most *Paragonostomum* species (cp. Fig. 32c, 33e). Asterisk denotes buccal cirrus. Arrow marks cirrus III/2. Broken lines connect cirri which originate from same anlage. Page 68.
AZM = adoral zone of membranelles, FC = frontal cirri, FT = frontoterminal cirri, FVC = frontoventral cirri of 18-cirri hypotrichs (dotted polygon), LMR = left marginal row, PVC = postoral ventral cirri, RMR = right marginal row, I–VI = frontal-ventral cirri anlagen.

in C-shaped pattern along left body margin; individual nodules separated by minute gaps, occasionally out of series, globular to ellipsoidal, on average 7 × 4 µm both in life and in protargol preparations; contain many small and large chromatin bodies. Usually a globular micronucleus each near ends of macronuclear series (Fig. 36a, e). Contractile vacuole in mid-body region left of midline, during diastole with two

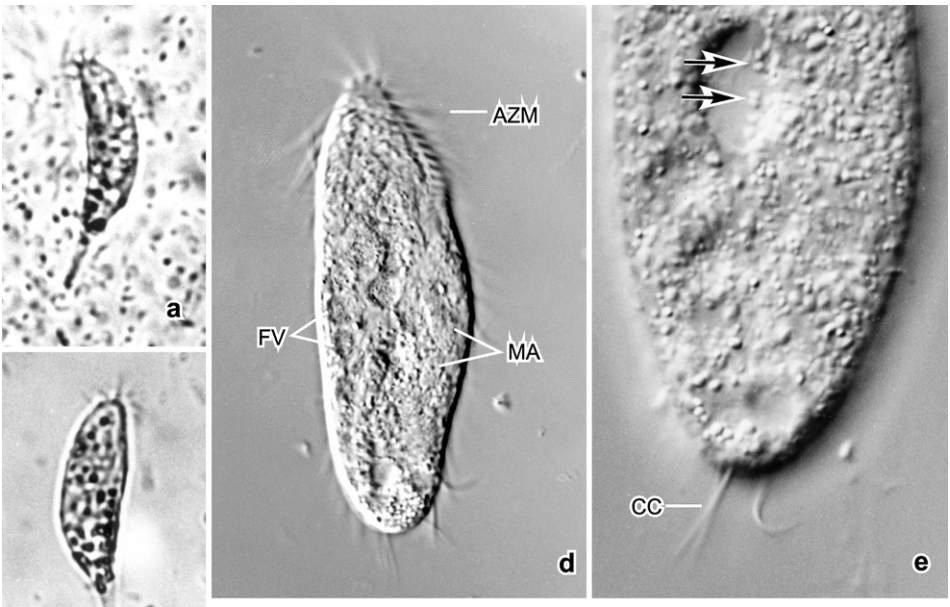

Fig. 37a, b *Paragonostomum (Paragonostomum) caudatum* (from Foissner et al. 2002a. Bright field micrograph). Freely motile specimens of Saudi Arabian population in dorsal (a) and ventral (b) view showing the conspicuous tail. Page 176.

Fig. 37c *Paragonostomum (Bigonostomum) binucleatum* (from Foissner et al. 2002a. Bright field micrograph). Freely motile specimen from type population in ventral view. Differs from *P. caudatum*, inter alia, by the less distinct tail. Page 192.

Fig. 37d, e *Paragonostomum simplex* (from Foissner et al. 2005. Differential interference contrast). Ventral overview (d) and dorsal detail (e) with cortical granules (arrows) clearly recognisable above the contractile vacuole. AZM = adoral zone of membranelles, CC = caudal cirri, FV = food vacuoles, MA = macronuclear nodules. Page 193.

long, thin collecting canals. Cortex very flexible, does not contain special granules in specimens from type locality (see remarks), while loosely to densely arranged, colourless, minute (≤0.50 × 0.25 µm) cortical granules (become up to 3 µm long, pink rods when methyl green-pyronin is added) occur in the Merckenstein and the Salzburg population (Fig. 36c, 37e). Cytoplasm colourless, densely granulated, usually packed with small food vacuoles about 5–10 µm across and up to 4 µm-sized lipid droplets mainly in rear cell end. Glides moderately rapidly on microscope slide and soil particles showing great flexibility.

Oral apparatus in *Gonostomum* pattern (for details, see *Gonostomum*). Adoral zone occupies only 37% (50% in most *Gonostomum* species) of body length on average, commences in mid of anterior cell end and extends along left body margin, performing abrupt right bend to plunge into buccal cavity near left margin; composed of

Table 16 Morphometric data on *Paragonostomum binucleatum* (bin, from Foissner et al. 2002a), *Paragonostomum caudatum* (cau, from Foissner et al. 2002a), *Paragonostomum multinucleatum* (mu1, type population; mu2, USA population; both from Foissner et al. 2002a; mu3, Slovakian population from Vdačny & Tirjaková 2006), and *Paragonostomum rarisetum* (rar, from Foissner et al. 2002a)

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Body or trunk, length [b]	bin	64.1	63.0	8.4	2.1	13.1	54.0	83.0	16
	cau	61.8	62.0	5.2	1.1	8.4	51.0	72.0	21
	mu1	59.6	61.0	7.1	1.6	11.9	48.0	72.0	19
	mu2	54.0	52.0	5.7	1.7	10.6	48.0	65.0	11
	mu3	60.8	62.5	10.1	3.2	16.5	46.9	78.1	10
	rar	59.9	60.0	3.8	1.0	6.4	52.0	68.0	15
Trunk, width	bin	21.8	21.0	3.5	0.9	16.0	14.0	27.0	15
	cau1	16.6	17.0	2.1	0.4	12.4	12.0	20.0	21
	mu1	15.8	16.0	1.3	0.3	8.4	13.0	18.0	20
	mu2	15.7	15.0	1.7	0.5	10.7	14.0	19.0	11
	mu3	12.1	12.5	2.7	0.9	22.7	7.8	15.6	10
	rar	16.7	16.0	2.0	0.5	12.1	13.0	22.0	15
Trunk or body length:width, ratio [b]	bin	3.0	2.9	0.7	0.2	21.5	2.1	4.0	15
	cau	3.8	3.7	0.4	0.1	11.7	3.0	4.6	21
	mu1	3.8	3.8	0.4	0.1	9.8	3.0	4.5	18
	mu2	3.5	3.5	0.4	0.1	12.9	2.7	4.1	11
	mu3	5.2	5.2	1.2	0.4	22.5	3.2	7.0	10
	rar	3.6	3.7	0.4	0.1	11.2	2.9	4.5	15
Tail, length [b]	cau	18.8	19.0	4.2	1.2	22.3	12.0	26.0	12
	mu3	12.7	12.5	3.9	1.2	31.0	7.8	18.0	10
	rar	17.5	17.0	3.7	1.0	21.0	13.0	23.0	15
Tail, width in mid-region [b]	cau	1.5	1.6	0.4	0.1	23.4	1.0	2.5	19
	mu3	3.0	2.8	0.7	0.2	23.9	2.2	4.7	10
	rar	2.3	2.0	–	–	–	2.0	3.0	15
Adoral zone of membranelles, length	bin	24.2	24.0	1.7	0.4	7.0	21.0	27.0	16
	cau	27.4	27.0	1.7	0.4	6.1	25.0	30.0	21
	mu1	21.2	22.0	2.3	0.5	10.9	16.0	26.0	21
	mu2	18.8	19.0	1.7	0.5	9.1	16.0	21.0	11
	mu3	18.9	18.0	2.1	0.6	10.9	16.4	22.7	10
	rar	21.3	21.0	0.8	0.2	3.8	20.0	23.0	15
Trunk or body length: length of adoral zone, ratio	bin	2.7	2.6	0.3	0.1	11.1	2.2	3.3	16
	cau	2.3	2.3	0.2	0.0	8.9	1.9	2.6	21
	mu1	2.8	2.9	0.4	0.1	12.5	2.2	3.6	19
	mu2	2.9	2.9	0.3	0.1	11.0	2.3	3.4	11
	mu3	3.2	3.3	0.3	0.1	10.5	2.7	3.7	10
	rar	2.8	2.8	0.2	0.1	7.6	2.4	3.2	15
Paroral, length	bin	6.1	6.0	0.7	0.2	11.6	5.0	8.0	15
	cau	8.2	8.0	1.1	0.2	13.1	7.0	11.0	19
	mu1	5.3	5.0	0.7	0.2	13.5	4.0	6.0	11
	mu3	4.0	4.0	0.6	0.2	15.5	3.1	4.7	10
	rar	7.3	8.0	0.9	0.2	12.1	6.0	8.0	15
Paroral kinetids, number	bin	6.4	7.0	1.0	0.3	15.4	4.0	8.0	15
	cau	9.4	9.0	1.2	0.3	13.1	7.0	12.0	20
	mu1	5.4	6.0	1.0	0.3	18.4	4.0	7.0	12
	mu2	5.3	5.0	1.6	0.5	29.5	3.0	8.0	11
	mu3	5.0	5.0	0.7	0.2	14.1	4.0	6.0	10
	rar	7.1	7.0	0.9	0.2	12.9	6.0	9.0	15

Table 16 Continued

Characteristics[a]	Species	mean	M	SD	SE	CV	Min	Max	n
Endoral, length	bin	9.6	10.0	0.7	0.2	7.0	8.0	10.0	11
	cau	7.9	8.0	1.2	0.3	14.8	6.0	10.0	17
	mu1	5.9	6.0	0.7	0.2	12.7	5.0	7.0	10
	mu3	5.8	5.9	1.0	0.3	18.1	4.7	7.8	10
	rar	4.7	4.5	0.9	0.3	18.9	4.0	7.0	12
Endoral kinetids, number	rar	7.9	8.0	1.0	0.3	12.6	6.0	9.0	10
Anterior body end to rearmost fronto-ventral cirrus, distance	bin	15.3	15.0	1.9	0.5	12.2	13.0	18.0	15
	cau	24.6	25.0	3.3	0.7	13.5	15.0	30.0	21
	mu1	12.2	12.0	1.6	0.4	13.5	9.0	15.0	20
	mu3	11.1	10.9	1.7	0.5	15.4	8.6	14.1	10
	rar	15.2	15.0	1.8	0.5	12.0	13.0	20.0	15
Anterior body end to buccal cirrus, distance	bin	10.4	10.0	–	–	–	10.0	11.0	16
	cau	13.4	13.0	1.0	0.2	7.3	12.0	15.0	21
	mu1	9.4	9.0	1.7	0.4	17.9	6.0	14.0	18
	mu3	12.2	10.9	2.0	0.6	16.4	10.2	15.6	10
	rar	9.4	10.0	1.9	0.5	20.0	7.0	14.0	15
Anterior body end to right marginal row, distance	bin	4.9	4.0	1.4	0.4	28.1	3.0	8.0	15
	cau	12.0	12.0	1.9	0.4	15.6	9.0	15.0	21
	mu1	3.5	3.5	0.9	0.2	24.4	2.0	5.0	16
	rar	7.0	7.0	1.6	0.4	22.9	4.0	10.0	15
Anterior body end to rear end of left marginal row, distance	cau	53.6	54.0	5.5	1.2	10.3	45.0	66.0	21
	mu1	56.0	57.0	6.4	1.8	11.4	45.0	64.0	13
	rar	59.9	60.0	3.8	1.0	6.4	52.0	68.0	15
Nuclear figure, length	bin	27.1	25.5	5.0	1.2	18.3	20.0	36.0	16
	mu1	28.9	29.0	3.0	0.6	10.3	22.0	35.0	21
	mu3	28.5	26.7	5.8	1.8	20.5	20.3	39.1	10
	rar	26.5	27.0	2.9	0.8	11.0	22.0	31.0	15
Macronuclear nodules, distance in between	bin	10.8	11.0	3.1	0.8	29.1	6.0	18.0	16
	rar	2.2	2.0	1.1	0.3	49.2	1.0	5.0	15
Anterior macronuclear nodule, length	bin	9.3	9.0	1.9	0.5	20.3	6.0	12.0	16
	cau	10.7	11.0	1.5	0.3	14.2	8.0	13.0	21
	mu1	5.0	5.0	1.3	0.3	26.8	3.0	8.0	21
	mu2	4.6	4.0	1.2	0.3	25.2	3.0	7.0	11
	mu3	6.0	6.1	1.2	0.4	20.7	4.0	7.8	10
	rar	11.4	11.0	1.4	0.4	11.9	10.0	14.0	15
Anterior macronuclear nodule, width	bin	5.7	6.0	0.6	0.2	10.6	4.0	6.0	16
	cau	4.6	5.0	0.7	0.2	16.3	3.0	6.0	21
	mu1	3.5	3.5	0.6	0.1	17.7	2.5	5.0	21
	mu2	3.2	3.0	–	–	–	3.0	4.0	11
	mu3	3.6	3.4	0.9	0.3	23.7	2.0	4.7	10
	rar	4.9	5.0	0.7	0.2	14.3	4.0	6.0	15
Macronuclear nodules, number	bin	2.0	2.0	0.0	0.0	0.0	2.0	2.0	16
	cau	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	mu1	6.1	7.0	1.8	0.4	25.5	4.0	9.0	21
	mu2	7.5	7.0	2.3	0.7	30.2	4.0	13.0	11
	mu3	7.2	8.0	1.9	0.6	26.6	4.0	9.0	10
	rar	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Anteriormost micronucleus, length	bin	1.6	1.5	–	–	–	1.5	2.0	15
	cau	1.7	1.6	–	–	–	1.2	2.4	21
	mu1	1.3	1.2	–	–	–	1.0	2.0	17

Table 16 Continued

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Anteriormost micronucleus, length	mu2	2.1	2.0	–	–	–	1.5	3.0	11
	rar	2.5	3.0	0.5	0.1	20.4	2.0	4.0	15
Anteriormost micronucleus, width	bin	1.5	1.5	–	–	–	1.5	2.0	15
	cau	1.5	1.6	–	–	–	1.0	1.6	21
	mu1	1.1	1.0	–	–	–	1.0	1.6	17
	mu2	1.6	1.5	–	–	–	1.3	2.0	11
	rar	1.8	2.0	–	–	–	1.5	2.0	15
Micronuclei, number	bin	1.8	2.0	–	–	–	1.0	2.0	15
	cau	1.9	2.0	–	–	–	1.0	2.0	21
	mu1 [c]	2.8	2.5	–	–	–	1.0	5.0	10
	mu2	1.4	1.0	–	–	–	1.0	2.0	11
	rar	1.9	2.0	0.5	0.1	27.7	1.0	3.0	15
Adoral membranelles, number	bin	20.5	21.0	2.3	0.6	11.4	16.0	23.0	16
	cau	18.7	19.0	1.2	0.3	6.6	17.0	21.0	21
	mu1	19.2	19.0	1.3	0.3	7.0	16.0	22.0	17
	mu2	14.5	14.0	1.1	0.3	7.8	13.0	17.0	11
	mu3	18.1	18.0	2.5	0.8	13.9	15.0	22.0	10
	rar	15.0	15.0	0.9	0.2	6.2	14.0	17.0	15
Frontal cirri, number	bin	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
	cau	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	mu1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	mu2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	mu3	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	rar	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Frontoterminal cirri, number	bin	2.1	2.0	–	–	–	2.0	3.0	14
	cau	4.4	4.0	–	–	–	4.0	5.0	21
	mu1	2.1	2.0	–	–	–	1.0	3.0	16
Frontoventral cirri, number	bin [d]	3.2	3.0	0.7	0.2	21.1	2.0	5.0	15
	cau [d]	6.7	6.0	1.0	0.2	14.9	5.0	9.0	22
	mu1 [d]	3.1	3.0	–	–	–	3.0	4.0	19
	mu2 [e]	5.4	5.0	–	–	–	5.0	7.0	11
	mu3	2.1	2.0	0.3	0.1	15.8	2.0	3.0	10
	rar [e]	6.5	6.0	0.8	0.2	12.8	5.0	8.0	15
Buccal cirri, number	bin	1.0	1.0	0.0	0.0	0.0	1.0	1.0	16
	cau	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	mu1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	18
	mu2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	mu3	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
	rar	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Right marginal cirri, number	bin	20.6	20.5	2.6	0.6	12.4	16.0	27.0	16
	cau	19.5	20.0	2.9	0.6	14.9	12.0	25.0	21
	mu1	21.6	22.0	3.6	1.0	16.5	17.0	29.0	14
	mu2	22.1	22.0	2.6	0.8	11.9	18.0	28.0	11
	mu3	23.0	23.0	2.4	0.8	10.6	18.0	26.0	10
	rar	21.1	21.0	3.3	0.9	15.8	13.0	25.0	15
Left marginal cirri, number	bin	14.6	15.0	1.7	0.4	11.9	12.0	17.0	16
	cau	11.1	11.0	1.7	0.4	15.1	8.0	14.0	21
	mu1	16.8	16.0	3.1	0.8	18.7	12.0	22.0	15
	mu2	16.5	16.0	2.4	0.7	14.6	13.0	21.0	11
	mu3	20.0	20.0	1.9	0.6	9.4	18.0	24.0	10

Table 16 Continued

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Left marginal cirri, number	rar	15.4	15.0	2.5	0.7	16.4	13.0	23.0	15
Dorsal kineties, number	bin [f]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
	cau	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	mu1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	mu2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	mu3	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	rar	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Dorsal kinety 2, number of kinetids	bin	10.9	9.5	1.2	0.4	12.0	9.0	12.0	8
	cau	14.5	14.0	1.9	0.5	13.1	12.0	18.0	16
	mu1	9.8	9.5	1.0	0.4	10.0	9.0	11.0	6
	mu3	18.9	20.0	2.1	0.7	11.4	16.0	21.0	10
	rar	10.9	11.0	1.2	0.3	11.2	9.0	13.0	15

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] In *P. caudatum* and *P. rarisetum*, the distance from anterior body end to tail base was measured (arrow in Fig. 30i), while in *P. binucleatum* and *P. multinucleatum* total body length is given because the tail is too indistinctly set off from body proper. Vdačny & Tirjaková (2006) measured "body, length", "body, width", "body length:width, ratio", and "body length:length of adoral zone".

[c] Uncertain because difficult to recognise.

[d] Cirri behind right frontal cirrus (e.g., III/2) included, frontoterminal cirri not included.

[e] Frontoterminal cirri included.

[f] Rarely occur specimens with four dorsal kineties.

an average of 20 membranelles with bases up to 4 µm wide in life. Buccal cavity very narrow and flat, right half and proximal portion of adoral zone covered by curved, hyaline buccal lip bearing paroral composed of an average of nine widely and equidistantly spaced, in life 6 µm long cilia. Endoral at right margin of buccal cavity, conspicuous because more than twice as long as paroral and composed of very narrowly spaced cilia. Pharyngeal fibres clearly recognisable in life and after protargol impregnation, extend obliquely to body midline and backwards (Fig. 36a, d, Table 17).

Cirral pattern stable, number of frontoventral cirri rather variable; all cirri, except frontal cirri, about 10 µm long in life and usually composed of six cilia arranged in two rows (Fig. 36a, d). Frontal cirri slightly enlarged, 13 µm long, arranged in *Gonostomum* pattern, that is, left cirrus distinctly displaced posteriad, middle cirrus somewhat larger than other two cirri; cirri frequently somewhat disorganised, that is, lack 1–3 cilia in variable position. Buccal cirrus invariably ahead of paroral. On average about eight frontoventral cirri (cirrus/cirri behind right frontal cirrus included; frontoterminal cirri not included) right of adoral zone (Table 17): in holotype specimen two cirri behind right frontal cirrus; short row of two cirri immediately right of previous row; four cirri form distinct row right of proximal portion of adoral zone

Table 17 Morphometric data on *Paragonostomum minuta* (min, from Kamra et al. 2008) and *Paragonostomum simplex* (si1, type population; si2, Salzburg population; both from Foissner et al. 2005)

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Body, length	min	33.0	–	–	–	–	–	–	?
	si1	76.9	78.0	9.7	2.1	12.6	62.0	92.0	21
	si2	79.9	82.0	8.2	2.1	10.3	60.0	93.0	15
Body, width	min	12.0	–	–	–	–	–	–	?
	si1	25.5	25.0	3.6	0.8	14.2	18.0	32.0	21
	si2	20.8	21.0	1.7	0.4	8.1	18.0	24.0	15
Body length:width, ratio	si1	3.1	3.0	0.5	0.1	17.2	2.3	4.1	21
	si2	3.9	3.9	0.5	0.1	11.9	3.1	4.7	15
Adoral zone of membranelles, length	si1	28.2	28.0	2.0	0.4	7.1	24.0	32.0	21
	si2	26.3	26.0	2.6	0.7	10.0	23.0	33.0	15
Body length:length of adoral zone, ratio	si1	2.7	2.6	0.4	0.1	14.4	2.2	3.8	21
	si2	3.1	3.2	0.5	0.1	14.3	2.2	3.8	15
Anterior body end to paroral, distance	min	9.4	–	–	–	–	–	–	?
Anterior body end to endoral, distance	min	9.4	–	–	–	–	–	–	?
Anterior body end to rearmost frontoventral cirrus, distance	si1	24.6	25.0	3.8	0.8	15.4	17.0	31.0	21
	si2	23.0	22.0	2.3	0.6	9.9	19.0	27.0	15
Anterior body end to buccal cirrus, distance	si1	13.4	13.0	0.8	0.2	6.1	11.0	14.0	21
	si2	11.6	12.0	1.6	0.4	13.8	8.0	14.0	15
Anterior body end to right marginal row, distance	si1	3.5	3.0	0.8	0.2	23.2	2.0	6.0	21
	si2	2.9	2.5	1.1	0.3	39.8	1.5	5.0	15
Anterior body end to posterior end of right marginal row, distance	si1	74.2	75.0	9.7	2.1	13.1	60.0	90.0	21
	si2	78.0	80.0	8.3	2.1	10.6	58.0	92.0	15
Nuclear figure, length	si1	51.9	51.0	6.0	1.3	11.5	41.0	61.0	21
	si2	51.5	52.0	5.3	1.4	10.2	43.0	59.0	15
Anteriormost macronuclear nodule, length	si1	6.5	7.0	1.5	0.3	23.7	3.0	10.0	21
	si2	5.0	5.0	0.7	0.2	14.5	4.0	6.0	15
Anteriormost macronuclear nodule, width	si1	4.4	4.0	0.8	0.2	16.9	3.0	6.0	21
	si2	3.8	4.0	0.7	0.2	18.9	3.0	5.0	15
Macronuclear nodules, number	min	–	–	–	–	–	7.0	8.0	?
	si1	10.4	11.0	2.5	0.6	24.2	8.0	15.0	21
	si2	10.7	11.0	1.4	0.4	13.4	9.0	14.0	15
Anteriormost micronucleus, length	si1	2.2	2.0	0.4	0.1	16.4	1.8	3.0	21
	si2	2.2	2.0	–	–	–	1.5	2.5	15
Anteriormost micronucleus, width	si1	1.9	2.0	0.2	0.1	10.6	1.3	2.2	21
	si2	1.8	2.0	–	–	–	1.5	2.0	15
Micronuclei, number	min	2.0	–	–	–	–	–	–	?
	si1	2.3	2.0	0.9	0.2	39.1	1.0	5.0	21
	si2	2.3	2.0	1.2	0.3	53.8	0.0	4.0	15
Adoral membranelles, number	min	20.0	–	–	–	–	–	–	?
	si1	19.7	20.0	1.0	0.2	4.9	18.0	22.0	21
	si2	19.5	19.0	1.6	0.4	8.4	17.0	23.0	15
Paroral, length	si1	5.2	5.0	0.8	0.2	15.7	4.0	6.0	21
	si2	4.7	5.0	0.7	0.2	14.9	4.0	6.0	15
Paroral kinetids, number	min	–	–	–	–	–	2.0	3.0	?
	si1	8.4	9.0	1.3	0.3	15.3	6.0	10.0	21
Paroral, distance between basal bodies	min	0.3	–	–	–	–	–	–	?
Frontal cirri, number	si1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	si2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Frontoterminal cirri, number	si1	3.8	4.0	0.5	0.1	14.3	3.0	5.0	21

Table 17 Continued

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Frontoterminal cirri, number	si2	4.1	4.0	1.0	0.3	24.0	3.0	6.0	15
Frontoventral cirri, number	min	7.0	–	–	–	–	–	–	?
	si1	8.3	8.0	1.6	0.4	19.1	6.0	13.0	21
	si2	7.7	8.0	1.6	0.4	21.1	5.0	10.0	15
Frontoventral row I, number of cirri	min	12.0	–	–	–	–	–	–	?
Buccal cirri, number	si1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	si2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Right marginal cirri, number	min	17.0	–	–	–	–	–	–	?
	si1	21.2	21.0	3.0	0.7	14.1	15.0	29.0	21
	si2	22.4	22.0	2.4	0.6	10.8	19.0	28.0	15
Left marginal cirri, number	min	4.0	–	–	–	–	–	–	?
	si1	16.4	16.0	2.7	0.6	16.5	12.0	23.0	21
	si2	16.7	17.0	1.2	0.3	7.0	15.0	19.0	15
Caudal cirri, number	min	3.0	–	–	–	–	–	–	?
	si1	2.9	3.0	–	–	–	2.0	3.0	21
	si2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Dorsal kineties, number	min	3.0	–	–	–	–	–	–	?
	si1	3.1	3.0	–	–	–	3.0	4.0	21
	si2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Kinetids in dorsal kinety 1, number	min	6.0	–	–	–	–	–	–	?
Kinetids in dorsal kinety 2, number	min	8.0	–	–	–	–	–	–	?
	si1	9.6	9.0	1.5	0.3	15.2	7.0	13.0	21
	si2	9.3	9.0	1.3	0.3	14.4	7.0	11.0	15
Kinetids in dorsal kinety 3, number	min	8.0	–	–	–	–	–	–	?

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean, ? = sample size not indicated (likely distinctly below 10). Data of *si1* and *si2* based on mounted, protargol-impregnated, and randomly selected specimens from non-flooded Petri dish cultures.

(Fig. 36d). On average four frontoterminal cirri in short row commencing right of right frontal cirrus. Frontoventral cirral pattern difficult to interpret without ontogenetic data; arrangement in holotype specimen indicates that in total six (I–VI) frontal-ventral cirri anlagen are present (Fig. 36j), whereas the frontoventral ciliature in the tailed *Paragonostomum* species and the two acaudate Indian *Paragonostomum* species are formed from five anlagen (anlage IV [or V?] lacking). Pretransverse ventral and transverse cirri lacking. Right marginal row only slightly shortened anteriorly, terminates on average at 96% of body length in type population (Table 17). Left marginal row commences at buccal vertex, terminates at rear end.

Dorsal bristles about 3 µm long in life, basically arranged in three kineties; frequently, however, with rather conspicuous irregularities, such as (i) anterior kinetids of kinety 3 slightly out of line or (ii) more or less complete fourth row, with kinetids partially turned upside down between rows 2 and 3 (Fig. 36e–i). Dorsal kineties slightly shortened posteriorly, while distinctly shortened anteriorly from left to right;

kinety 3 anteriorly only slightly shortened and curved to cell's midline. Caudal cirri at rear end, often right of midline; moderately distinct in life (Fig. 36a, e, 37e).

Occurrence and ecology: Very likely confined to terrestrial habitats. Type locality of *P. simplex* is the soil (geology: dolomite; soil type: rendzic leptosol; humus type: calcareous moder) of a *Pinus nigra* forest in the Stampfltal (16°02'E 47°53'N) near the city of Vienna, Austria (Foissner et al. 2005). We found it also in a second Pine forest soil (Merckenstein) near the type locality (Foissner et al. 2005). Erna Aescht found *P. simplex* in the soil of beech forest of a suburb of the city of Salzburg, Austria (Table 17; Foissner et al. 2005). *Paragonostomum simplex* developed soon after rewetting the sample, indicating that it is more r- than K-selected (details on r- and K-selection in soil ciliates, see Foissner 1987a, Lüftenegger et al. 1985, Foissner et al. 2005).

Paragonostomum simplex feeds mainly on bacteria; rarely fungal spores and/or green algae are recognisable in food vacuoles up to 6 µm across (Foissner et al. 2005).

Paragonostomum minuta Kamra, Kumar & Sapra, 2008
(Fig. 38a–c, Table 17)

2005 ***Paragonostomum minuta*** **sp nov** [1] – Kamra, Kumar & Sapra, Indian J. Microbiol., 48: 379, Fig. 5a–d, 10a–f (Fig. 38a–c; original description; one protargol slide is deposited in the Natural History Museum in London; no accession number given).

Nomenclature: The species-group name *minut·us, -a, -um* (Latin adjective [m; f; n]; very small, tiny) refers to the fact that *P. minuta* is the smallest species of the genus (Kamra et al. 2008).

Remarks: The present species was assigned to *Paragonostomum* because transverse cirri are absent; however, it lacks the tailed posterior body portion of the typical *Paragonostomum* species. The second *Paragonostomum* species described by Kamra et al. (2008), *P. ghangriai*, has to be transferred to *Neowallackia* because its cirral pattern is identical with that of *N. franzi* (previously *Gonostomum franzi*), which lacks caudal cirri. Kamra et al. (2008) obviously misinterpreted the rearmost left marginal cirri as caudal cirri in *P. ghangriai*. Perhaps the caudal cirri of *P. minuta* are also misinterpreted marginal cirri, making its generic assignment uncertain. This assumption is supported by the very small paroral composed of two or three cilia only, a feature also present in *N. franzi* (Fig. 53a). However, since *P. minuta* lacks the second frontoventral row, which is present in all *Neowallackia* species, I preliminary retain the original generic assignment.

[1] Kamra et al. (2008) provided the following diagnosis: Body oblong without a tail, pointed posterior end; mean body size of protargol stained non dividers 33 × 12 µm; 7–8 oval macronuclei, 2 spherical micronuclei; AZM 50% of body length, PM with 2–3 cilia, EM made of tightly packed cilia; frontal ciliature lacks transverse cirri, 7 cirri in the frontal (oral) region and one fronto-terminal row with 12 cirri; one row each of LMC and RMC with 4 and 17 cirri on an average; 3 DKs and 3 CCs; all cirri highly hypertrophied and long.

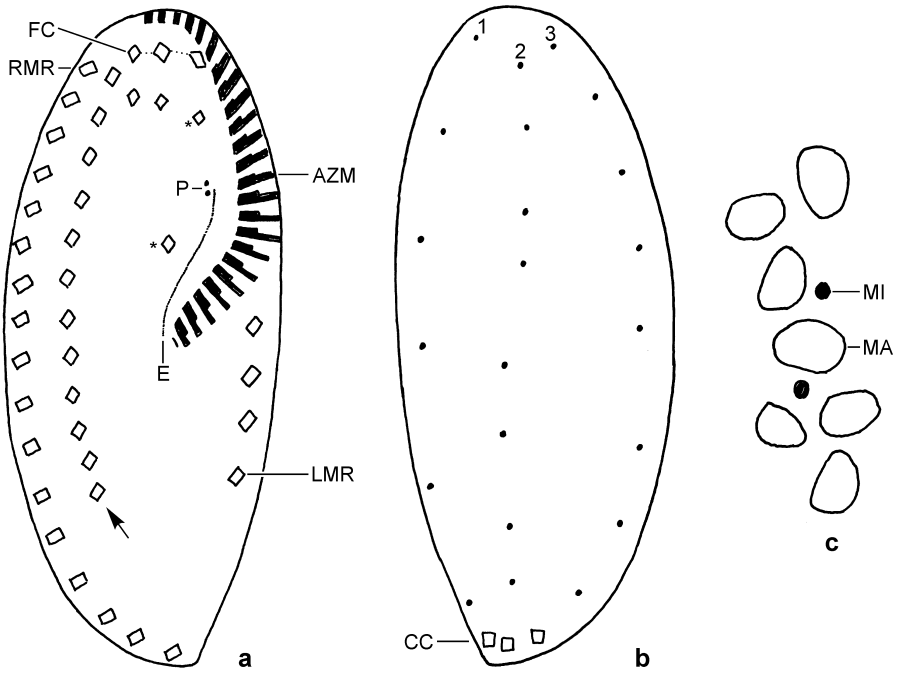

Fig. 38a–c *Paragonostomum minuta* (after Kamra et al. 2008. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus, 30 µm. Arrow marks rear end of frontoventral row. One of the two cirri marked with an asterisk is the buccal cirrus. Frontal cirri connected by dotted line. Ontogenetic data are needed for correct interpretation of the frontal ciliature. AZM = adoral zone of membranelles, CC = caudal cirri, E = endoral, FC = frontal cirri, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = right marginal row, 1–3 = dorsal kineties. Page 204.

The habitus of *P. minuta* is somewhat reminiscent of a degenerate population. Further studies are needed to show whether or not it is indeed a valid species or only a degenerate stage of, for example, *N. ghangriai*. *Gonostomum gonostomoidum*, which also has a long frontoventral row, is larger and has transverse cirri (Fig. 25a–j).

Morphology: Kamra et al. (2008) found only few specimens and therefore could not provide a detailed morphometric analysis. Body size on average 33 × 12 µm in protargol preparations. Body oblong with anterior end rounded and posterior end somewhat pointed; right margin more convex than left one. 7–8 roughly ellipsoidal macronuclear nodules arranged as shown in Fig. 38c, likely about in midline or slightly left of it; two spherical micronuclei. Contractile vacuole near mid-body close to proximal end of adoral zone, that is, obviously in ordinary position. Cortical granules few and scattered; size and colour not mentioned. Cells often attached to soil particles.

Oral apparatus in *Gonostomum* pattern (see *Gonostomum* [p. 58] and/or Berger 1999). Adoral zone occupies roughly 50% of body length, composed of about 20

membranelles made up of 5.4 µm long cilia. Paroral consist of 2–3 cilia (Table 17), arranged at anterior end of endoral, which is of usual structure, that is, composed of narrowly spaced cilia. Buccal area obviously small and flat.

Cirral pattern as shown in Fig. 38a, somewhat difficult to interpret without ontogenetic data: three slightly enlarged frontal cirri with left one not distinctly displaced posteriad as in other gonostomatids. One cirrus (buccal cirrus?) right of middle portion of endoral. Frontoventral row runs along right marginal row, composed of 12 cirri, terminates at 75% of body length in specimen illustrated. Transverse cirri lacking. Right marginal row commences at level of frontal cirri, terminates at rear end of cell; left marginal row begins left of proximal portion of adoral zone, very short, that is, terminates about at same level as frontoventral row. Cirri very long and well developed; cilia of frontal cirri 5–8 µm long, marginal cirri 7–12.5 µm, and caudal cirri 8–12 µm.

Three bipolar dorsal kineties composed of widely spaced, 3 µm long bristles (Table 17). Three caudal cirri at end of cell (Fig. 38b). According to a micrograph (Fig. 10f in Kamra et al. 2008), these seem to be indeed caudal cirri; however, ontogenetic data are needed for the final classification because *Paragonostomum* (very likely) has caudal cirri, whereas *Neowallackia* has no such cirri (see remarks).

Occurrence and ecology: The type locality of *P. minuta* is the Valley of Flowers National Park (31°41'–30°48' N 79°33'–79°46'E), Himalayan region, India, where Kamra et al. (2008) discovered it in soil samples. No details provided.

Wallackia Foissner, 1976

1976 ***Wallackia* nov. gen.**[1] – Foissner, Acta Protozool., 15: 390 (original description). Type species (by original designation and monotypy): *Wallackia schiffmanni* Foissner, 1976.
1979 ***Wallackia* Foissner, 1976** – Jankowski, Trudy zool. Inst., Leningr., 86: 84 (catalogue of hypotrich genera).
1979 ***Wallackia* Foissner, 1976** – Tuffrau, Trans. Am. microsc. Soc., 98: 526 (classification of hypotrichs).
1979 ***Wallackia* Foissner, 1977** – Corliss, Ciliated Protozoa, p. 310 (classification of ciliates; incorrect year).
1983 ***Wallackia* Foissner, 1976** – Curds, Gates & Roberts, British and other freshwater ciliated protozoa, p. 422 (guide to freshwater genera).
1985 ***Wallackia*** – Small & Lynn, Ciliophora, p. 455 (guide to ciliate genera).
1987 ***Wallackia* Foissner, 1977** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (classification of hypotrichs; incorrect year).
1994 ***Wallackia*** – Corliss, Acta Protozool., 33: 15 (classification of protists).

[1] Foissner (1976) provided the following diagnosis: Oxytrichidae mit je einer vollständigen rechten und einer in der Höhe des Cytostoms beginnenden linken Reihe von Marginalcirren, die caudad nicht geschlossen sind. Zwei gerade verlaufende, durchgehende Reihen von Ventralcirren, die ohne deutliche Unterbrechung in die leicht verstärkten Transversalcirren übergehen. Rechts der adoralen Zone noch zwei regelmäßig angeordnete Reihen von Frontalcirren, von denen die vorderen leicht verstärkt und griffelartig ausgebildet sind. Die Caudalcirren sind lang und entspringen in rohrartigen Verlängerungen des Ektoplasmas. Der Körper ist schlank-oval und mäßig abgeflacht. Der Makronucleus ist zweiteilig und besitzt je einen Mikronucleus.

1994 ***Wallackia* Foissner 1976** – Tuffrau & Fleury, Traite de Zoologie, 2: 141 (classification of hypotrichs).
1999 ***Wallackia* Foissner, 1976** – Shi, Song & Shi, Progress in protozoology, p. 107 (classification of hypotrichs).
1999 ***Wallackia* Foissner, 1976** – Shi, Acta Zootax. sinica, 24: 258 (classification of hypotrichs).
2001 ***Wallackia* Foissner 1976** – Aescht, Denisia, 1: 175 (catalogue of generic names of ciliates).
2001 ***Wallackia* Foissner, 1976** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 102 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).
2002 ***Wallackia* Foissner, 1977** – Lynn & Small, Ciliophora, p. 456 (guide to ciliate genera; incorrect year).
2006 ***Wallackia* Foissner, 1960** – Berger, Monographiae biol., 85: 1214 (brief note on exclusion from urostyloids).
2007 ***Wallackia* Foissner, 1976** – Jankowski, Ciliophora, p. 469 (classification of ciliates).
2008 ***Wallackia* Foissner, 1960** – Berger, Monographiae biol., 88: 470 (brief note on exclusion from amphisiellids).
2008 ***Wallackia* Foissner, 1976** – Lynn, Ciliated protozoa, p. 357 (classification of ciliates).

Nomenclature: Foissner (1976, p. 390) dedicated this genus to Franz Friedrich Wallack, who planned the Großglockner-Hochalpenstraße, a famous alpine road in Austria near the type locality of the type species. Foissner (1976, p. 388) used the term "Genotyp" to fix *W. schiffmanni* as type species. However, according to the relevant code, this term should never be used for this purpose (ICZN 1964, Recommendation 67A). Since this was only a recommendation, the type fixation is by original designation. Feminine gender (Aescht 2001, p. 305).

Characterisation (A = supposed apomorphy): Gonostomatidae with five (I–V; A) frontoventral rows/anlagen (anlage I, forming undulating membranes and left frontal cirrus, included). Anlagen II–V form distinctly more cirri than in 18-cirri hypotrichs (A). Contractile vacuole distinctly displaced inwards. Cortical granules (extrusomes) ellipsoidal to rod-shaped forming more or less conspicuous seam (*W. schiffmanni*, *W. bujoreani*) or lacking (*W. elegans*). Transverse cirri sensu stricto lacking. Three bipolar dorsal kineties, that is, dorsomarginal kineties and dorsal kinety fragmentation lacking. Caudal cirri usually shaped like a Pasteur pipette. Anlage I of proter originates de novo (A). Anlage II of opisthe is the anterior fragment of anlage I of opisthe (A).

Additional characters: Body length 50–100 µm; body flexible. Two macronuclear nodules. Terrestrial or semiterrestrial. Dorsal kinety 1 more or less distinctly shortened anteriorly (*W. schiffmanni*?).

Remarks: Foissner (1976) classified *Wallackia* in the Oxytrichidae and supposed a close relationship with *Gonostomum* (p. 58) and *Trachelochaeta* (p. 300) because of similarities in the cirral pattern. This classification was retained by Jankowski (2007). I assign *Wallackia* to the Gonostomatidae mainly because of the gonostomatid oral apparatus and the lack of dorsal kinety fragmentation and dorsomarginal rows. The simple dorsal kinety pattern was obviously taken over from the ground pattern of the hypotrichs and suggests a classification in the non-dorsomarginalian hypotrichs (Berger 2008). Such a position is also supported by molecular data (for details, see *Gonostomum*). *Kahliella*, which also has a more or

less distinct gonostomatid oral apparatus, has a dorsomarginal kinety indicating that it belongs to the non-oxytrichid Dorsomarginalia (p. 347). However, this assumption implies that this type of oral apparatus has evolved two times independently.

Gonostomum differs from *Wallackia* by the presence of true transverse cirri. Moreover, most species have a cirral pattern which – at least partially – closely resembles that of 18-cirri hypotrichs, including the formation from six (I–VI) anlagen (see p. 58). By contrast, *Wallackia* lacks the plesiomorphic 18-cirri pattern and obviously has lost one of the three rightmost frontal-ventral-transverse cirri anlagen IV–VI. Unfortunately, I do not know which of these anlagen is lacking. When further studies demonstrate that it is the same as in *Neowallackia* then the loss of this anlage could be interpreted as synapomorphy.

Trachelochaeta is little known because the type species *T. bryophila* Šrámek-Hušek, 1954 is not described after silver impregnation (p. 300). According to the original description, the anterior body portion is distinctly narrowed (cephalised), the frontoventral rows IV and V are distinctly shortened anteriorly, the transverse cirri are prominent because clearly recognisable even in life, and the four caudal cirri are very long. Hemberger (1982, p. 44) synonymised *Wallackia* with *Trachelochaeta* because he put *W. schiffmanni* into the synonymy of "*Trachelochaeta bujoreani*". However, *Trachelochaeta bryophila*, type of *Trachelochaeta*, has distinct transverse cirri (vs. lacking in *Wallackia*), anteriorly shortened frontoventral rows IV and V (vs. unshortened), and a narrowed anterior body portion (vs. not narrowed). Thus, synonymy of *Wallackia* and *Trachelochaeta* is very unlikely.

Orthoamphisiella Eigner & Foissner, 1991 lacks a gonostomatid oral apparatus and caudal cirri, has only two dorsal kineties, and the right parental frontoventral row (= row V) forms only a single anlage (vs. two in *Wallackia*; Eigner & Foissner 1993; p. 620).

Cladotricha is perhaps the most similar genus because it also has two long frontoventral rows (p. 235). However, the type species of *Cladotricha* is not yet described in detail so that a serious comparison is impossible at present. The shape of the caudal cirri (shaped like a Pasteur-pipette in *Wallackia* vs. normal) and the habitat (usually limnetic or terrestrial vs. usually highly saline) are the key differentiators.

Small & Lynn (1985) assigned *Wallackia* to the newly established Gonostomatidae, a group which was never accepted by later workers (e.g., Berger 1999, Lynn & Small 2002, Lynn 2008). By contrast, Shi et al. (1999) and Shi (1999) classified *Wallackia* in the Keronopsidae Jankowski, 1979. However, *Keronopsis* Penard, 1922 and its sistergroup *Paraholosticha* Wenzel, 1953 lack the gonostomatid oral apparatus, have a different cirral pattern (e.g., frontal cirri arranged in a corona), and divide in cysts, strongly indicating that the relationship to *Wallackia* is not very close.

Corliss (1977, p. 137; 1979), Tuffrau (1979, 1987), and Curds et al. (1983) assigned *Wallackia* to the Holostichidae, a group of urostyloids (for review, see Berger 2006a). Since *Wallackia* lacks a midventral pattern, this classification is not comprehensible. Later, Foissner & Foissner (1988, p. 83), Lynn & Small (2002), and Lynn

(2008) assigned it to the Kahliellidae whose type genus has, however, a dorsomarginal kinety. Tuffrau & Fleury (1994, p. 141) transferred *Wallackia* to the Amphisiellidae, but in this group the rightmost frontoventral row is a mixed row originating from two or three different anlagen (Eigner 1994; for review, see Berger 2008). By contrast, in *Wallackia*, which has only five anlagen, the rightmost row is formed from a single anlage.

Species included in *Wallackia* (alphabetically arranged basionyms are given): (1) *Paraholosticha bujoreani* Lepsi, 1951; (2) *Wallackia elegans* Foissner, Agatha & Berger, 2002; (3) *Wallackia schiffmanni* Foissner, 1976 (type species).

Key to *Wallackia* species

If you cannot identify your specimens with the key below, see also *Neowallackia* (caudal cirri lacking; p. 280), *Kahliella* (more cirral rows including parental rows with widely spaced cirri; p. 347), *Gonostomum* (caudal and transverse cirri present; p. 58 and Berger 1999, p. 367), *Paragonostomum* (few frontoventral cirri; body tailed; p. 172), or *Cladotricha* (highly saline habitat; p. 235).

1 Posterior body portion tail-like narrowed and curved rightwards (live observation needed! Fig. 42a, l) . . . . . *Wallackia elegans* (p. 227)
- Body shape not as above, because rear cell end more or less broadly rounded (Fig. 39a, 40a). **2**
2 Limnetic or semiterrestrial; cortical granules rod-shaped; caudal cirri widely separated; posterior body end with (elongated) dorsal bristles (Fig. 39a, b, d). . . . . *Wallackia schiffmanni* (p. 209)
- Terrestrial; cortical granules short ellipsoidal; caudal cirri narrowly spaced; posterior body end without distinct dorsal bristles (Fig. 40a, b, g, h). . . . . *Wallackia bujoreani* (p. 212)

Wallackia schiffmanni Foissner, 1976
(Fig. 39a–d)

1976 ***Wallackia schiffmanni* nov. gen., nov. spec.** – Foissner, Acta Protozool., 15: 388, Abb. 1–3, Tabelle 1 (Fig. 39a–d; original description, no formal diagnosis provided; no type material available, Aescht 2008, p. 196).
1979 ***Wallackia schiffmanni*** – Borror, Trans. Am. microsc. Soc., 98: 161 (brief discussion of ciliature).
1983 ***Wallackia*** – Curds, Gates & Roberts, British and other freshwater ciliated protozoa, p. 423 (redrawing of Fig. 39a; guide to freshwater genera).
1985 ***Wallackia schiffmanni*** – Small & Lynn, Ciliophora, p. 455, Fig. 21 (Fig. 39a; guide to ciliate genera).
1999 ***Wallackia*** – Shi, Song & Shi, Progress in protozoology, p. 107, Fig. 31 (schematic redrawing of Fig. 39a; classification of hypotrichs).

1999 ***Wallackia*** – Shi, Acta Zootax. sinica, 24: 258, Fig. 30 (schematic redrawing of Fig. 39a; classification of hypotrichs).

2001 ***Wallackia schiffmanni* Foissner, 1976** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 102 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).

Nomenclature: Foissner (1976, p. 388) dedicated this species to Hubert Schiffmann with whom he published some papers about peritrichs (e.g., Foissner & Schiffmann 1974, 1979). Type species of *Wallackia*. *Wallackia schiffsmanni* in Jankowski (1979, p. 84) is an incorrect subsequent spelling.

Remarks: For a detailed comparison with congeners, see key and remarks at *W. bujoreani* (most similar species) and *W. elegans*. The original description is mainly based on live observations; only the nuclear apparatus has been stained with orcein-acetic acid and the silverline system has been impregnated with the dry silver nitrate method. Thus, a detailed redescription is necessary to show the differences to *W. bujoreani* more clearly because synonymy with *W. bujoreani* cannot be excluded one hundred per cent at the present state of knowledge (see *W. bujoreani*).

Morphology: As mentioned above, most data, including infraciliature, are based on live observations. Thus, some details of the cirral pattern, the oral ciliature (undulating membranes), and the dorsal kinety pattern must not be overinterpreted. Body size 85–100 × 25–33 µm, body length:width ratio of specimen illustrated 3.1:1 (Fig. 39a). Body outline elliptical, posterior end broader rounded than anterior. Body distinctly (about 3:1) flattened dorsoventrally because 25–33 µm wide and 7–10 µm high. Macronuclear nodules ellipsoidal (Fig. 39a; according to text of original description they are reniform), about 10 µm long, finely granulated; according to Fig. 39a arranged about in midline (possibly the nodules are somewhat left of midline). One large (7 µm!), elongate ellipsoidal micronucleus attached to left side of each macronuclear nodule (Fig. 39a). Contractile vacuole right(!) of proximal portion of adoral zone, empties into cytopharynx[1] (Fig. 39a) Cortical granules (extrusomes?) rod-shaped, rather regularly arranged, form seam (Fig. 39b); become indistinct under high cover glass pressure. Cells opaque because cytoplasm packed with strongly refractive granules of unknown origin; granules colourless, 2–4 µm across, and irregularly round (Fig. 39b). Food vacuoles small and few in number. Creeps on debris particles, moves hastily to and fro; rests only for a short period and then spreads cirri; movement thus more or less jerky, never continuously gliding.

Adoral zone occupies about 50% of body length (55% in specimen illustrated), gonostomatid (for details, see p. 15 and Berger 1999), that is, commences near midline of anterior body end, extends straight along left body margin, performing abrupt bend and slight clockwise rotation to plunge into buccal cavity near left body margin. Number of membranelles likely somewhat overestimated in illustration (Fig. 39a). Membranelles comparatively short. “Undulating membrane” small and composed of several rows of cilia which stick together (it is unclear which membrane [paroral or endoral] Foissner saw). Pharyngeal fibres not seen.

[1] Foissner (1976) observed this unusual position more than one time; however, he also noted that this feature should be checked.

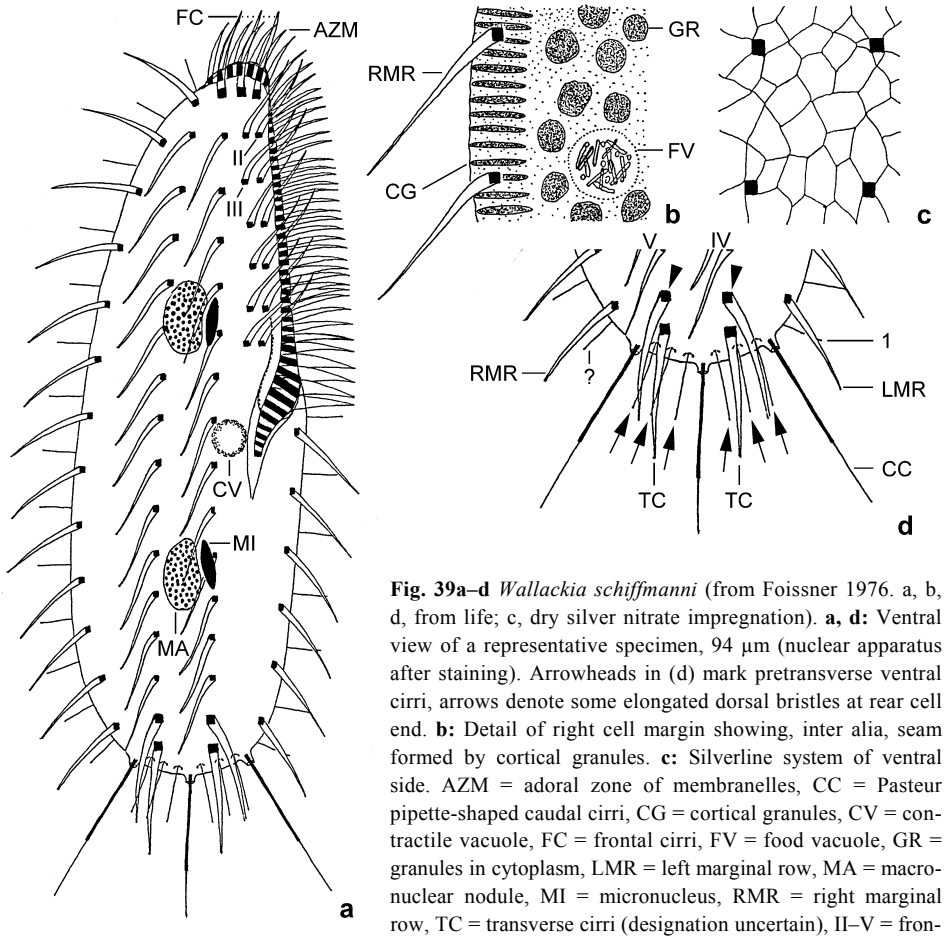

Fig. 39a–d *Wallackia schiffmanni* (from Foissner 1976. a, b, d, from life; c, dry silver nitrate impregnation). **a, d:** Ventral view of a representative specimen, 94 µm (nuclear apparatus after staining). Arrowheads in (d) mark pretransverse ventral cirri, arrows denote some elongated dorsal bristles at rear cell end. **b:** Detail of right cell margin showing, inter alia, seam formed by cortical granules. **c:** Silverline system of ventral side. AZM = adoral zone of membranelles, CC = Pasteur pipette-shaped caudal cirri, CG = cortical granules, CV = contractile vacuole, FC = frontal cirri, FV = food vacuole, GR = granules in cytoplasm, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row, TC = transverse cirri (designation uncertain), II–V = frontoventral cirral rows, 1 = leftmost dorsal kinety, ? = rightmost dorsal kinety (number of kineties not confirmed by staining). Page 209.

Cirral pattern described only after live observations (Fig. 39a, d). All cirri very fine, about 12–15 µm long, can be spread. Frontal cirri slightly enlarged, somewhat set off from remaining cirri of frontoventral rows. Two cirral rows (= rows II and III), each with 5–7 cirri, close to straight portion of adoral zone. Frontoventral rows IV and V commence slightly behind level of frontal cirri, extend to near rear cell end; rearmost two cirri of both rows obviously slightly enlarged, somewhat set off and curved inwards, thus designated as transverse cirri in original description. However, per definition, only the rearmost cirrus of each row can be designated as transverse cirrus; the cirrus ahead of it should be termed pretransverse ventral cirrus. According to Foissner (1976), the cilia forming these cirri are stronger than the cilia forming the marginal or ventral cirri (morphogenetic data are needed to show whether these cirri show a specific feature so that the designation as transverse cirri is justi-

fied). Marginal rows close to cell margin, cirri comparatively widely spaced; left row commences, as is usual, left of proximal portion of adoral zone, ends, like right row, subterminally; right row begins slightly behind level of frontal cirri (Fig. 39a, d).

Dorsal cilia about 5 µm long; cilia at rear cell end up to 10 µm long and emerging from ectoplasmic pits; according to Foissner (1976) arranged in 4–6 rows, a feature doubted by Foissner himself in a later paper (Foissner et al. 2002a, p. 649). Probably, *Wallackia schiffmanni* has, like *W. bujoreani* and *W. elegans*, only three kineties, as also indicated by the presence of only three caudal cirri (however, an increased number cannot be excluded). Each three dorsal bristles between two caudal cirri. Caudal cirri conspicuous because widely spaced, about 20 µm long, and, most important, shaped like a Pasteur pipette (Fig. 39a, d).

Silverline system, as is other hypotrichs, that is, composed of fine (1–5 µm) meshes (Fig. 39c).

Occurrence and ecology: Possibly confined to limnetic habitats (Foissner & Foissner 1988, p. 83). Type locality of *Wallackia schiffmanni* is the Großglockner area (Austrian Central Alps) near the so-called "Hochtor" (2575 m above sea-level) at the border of Salzburg and Carinthia (see Krainer 1999, p. 671) at the Großglockner-Hochalpenstrasse, a famous alpine road. Foissner (1976) found it there in an infusion of hay from a small pond with snow-water (= site 39 near the "Knappenstube" in Foissner 1980; likely such melt-water ponds have a distinct terrestrial influence). At first, only few specimens were present; with increasing abundance of bacteria, the abundance of *W. schiffmanni* also increased. After two weeks, the population disappeared. According to Foissner (1980, p. 111), it appeared in two further sites of the same area, namely in a perennial pond in the so-called "Hexenküche" (detailed description of this site, see Foissner & Adam 1979, p. 155) and a melt water pool (= site 53 in Foissner 1980) near the Wallackhaus, a hotel. No further records published. According to Foissner (1976), *Wallackia schiffmanni* inhabits beta- to alpha-mesosaprobic waters. Foissner et al. (1982a, p. 97) provided some autecological data, for example, 7.7–12.0°C, pH 4.8–4.9, 88–113% O_2. Feeds on bacteria (Foissner 1976).

Wallackia bujoreani (Lepsi, 1951) Berger & Foissner, 1989
(Fig. 40a–i, 41a–p, Table 18)

1951 ***Paraholosticha bujoreani* n. sp.** – Lepsi, Buletin sti. Acad. Repub. pop. rom., 3: 520, Fig. 12 (Fig. 40e; original description; no formal diagnosis provided and very likely no type material available).

1982 ***Trachelochaeta bujoreani* (Lepsi, 1951) n. comb.**[1] – Hemberger, Dissertation[2], p. 44 (revision and [nomenclaturally invalid?] combination with *Trachelochaeta*; see footnotes).

[1] This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3). See next footnote.

[2] According to the ICZN (1964), dissertations are not explicitly mentioned under Article 9, which describes all those acts that do not constitute a publication within the meaning of the Code. Thus, Hemberger's (1982) thesis, for which the ICZN (1964) has to be applied, could possibly also be nomenclaturally relevant. Unfortunately, the situation is rather complicated and almost each thesis would need a de-

1989 ***Wallackia bujoreani* (Lepsi, 1951) nov. comb.** – Berger & Foissner, Bull Br. Mus. nat. Hist. (Zool.), 55: 25, Fig. 19–22, Tables 1, 5 (Fig. 40a–d; redescription; a neotype slide [accession number 1988:2:1:28] has been deposited in the British Museum [Natural History] in London; see nomenclature).

2001 ***Wallackia bujoreani* (Lepsi, 1951) Berger and Foissner, 1989** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 67 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).

2002 ***Wallackia bujoreani*** – Lynn & Small, Ciliophora, p. 456, Fig. 47A, B (Fig. 40c, d; guide to ciliate genera).

2002 ***Wallackia bujoreani* (Lepsi, 1951) Berger & Foissner, 1989** – Foissner, Agatha & Berger, Denisia, 5: 635, Fig. 142a–g, 143a–p, 398l (Fig. 40f–i, 41a–p; description of Namibian population and cell division).

Nomenclature: I did not find a dedication or derivation of the name in the original description, which is in Romanian. Obviously, Lepsi (1951) dedicated this species to a person; Bujorean is a common surname in Romania (see internet).

Hemberger (1982, p. 44) synonymised *W. schiffmanni* Foissner, 1976 with *W. bujoreani* and simultaneously transferred it to *Trachelochaeta*, a valid, monotypic group treated in the present book (p. 300). Thus, Hemberger also synonymised *Wallackia* with *Trachelochaeta*.

Supplement to the neotypification of *W. bujoreani* by Berger & Foissner (1989a): In 1989, we deposited a neotype slide in the British Museum (Berger & Foissner 1989a, p. 20), but did not publish all qualifying conditions necessary for a neotypification (ICZN 1985, Article 75). To clear up this unsatisfactory condition, the neotypification is supplemented:

(i) Synonymy of *W. bujoreani* and *W. schiffmanni* (type species) cannot be excluded (details see remarks). Thus, a neotype of *Wallackia bujoreani* was fixed to define this taxon objectively. Unfortunately, no type material of *W. schiffmanni* is available (Aescht 2008, p. 196) to compare these two species on the basis of permanent slides. Further studies are needed to clear up the complex situation finally.

(ii) For separation of *W. bujoreani* from *W. schiffmanni* and *W. elegans*, see key above and remarks below.

(iii) For a detailed description of the neotype specimen and population, see Berger & Foissner (1989a) and morphology section below.

(iv) It is generally known that Lepsi (1951) made live observations only, that is, there is little doubt that a usable permanent type slide is not available. Thus, no steps have been undertaken to trace type slides.

(v) The neotype population agrees with the original description by Lepsi (1951) in the general morphology, the cirral pattern, the position of the contractile vacuole,

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tailed analysis whether or not it meets the requirements of publication (P. Tubbs, ICZN, Natural History Museum, London, pers. comm.). Thus, I do not accept Hemberger (1982) in the present case. The new taxa described by Hemberger (1982) have been again described by Hemberger (1985), which is the nomenclaturally valid paper. However, I include the thesis in the list of synonyms because it is one of the most important papers on hypotrichs since Kahl (1932). To avoid nomenclatural problems each new name/combination mentioned by Hemberger (1982) is individually disclaimed for nomenclatural purposes (see corresponding footnotes).

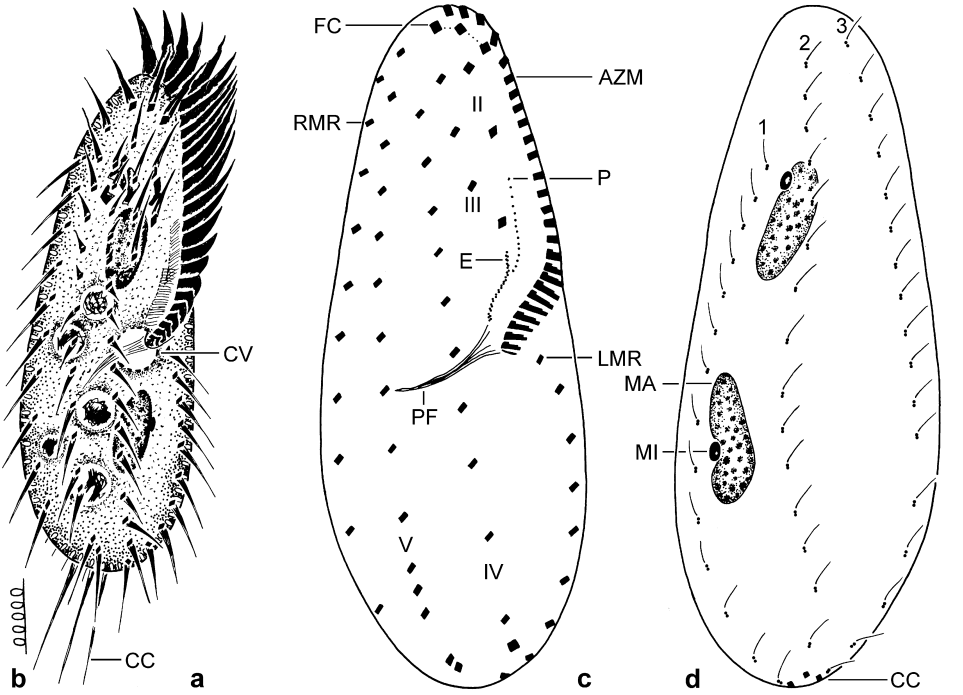


Fig. 40a–d *Wallackia bujoreani* (neotype population from Berger & Foissner 1989a. a, b, from life; c, d, protargol impregnation). **a:** Ventral view of a representative specimen, 70 µm. Note the *Gonostomum*-like oral apparatus. **b:** Colourless, short ellipsoid cortical granules (extrusomes; about 1.5 µm across) close beneath the pellicle. **c, d:** Infraciliature of ventral and dorsal side and nuclear apparatus of neotype specimen, 65 µm. AZM = adoral zone of membranelles, CC = caudal cirri, CV = inwards shifted contractile vacuole, E = endoral, FC = frontal cirri, LMR = anterior end of left marginal row, MA = rear macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = right marginal row, I–V = frontoventral rows, 1–3 = dorsal kineties. Page 212.

the presence of cortical granules forming a seam, and the habitat, strongly indicating that they belong to the same species. However, it cannot be excluded that *W. bujoreani* and *W. schiffmanni* are synonyms (see below).

(vi) The distance between the old (Timisoare, Romania) and new (Ajaccio, Island Corsica) type locality is about 1000 km, which is not very near, but at least on the same continent. In addition, both populations are from terrestrial habitats.

(vii) The neotype slide is deposited in the British Museum of Natural History, London (accession number 1988:2:1:28) since 1988.

Remarks: Lepsi (1951) established this species in *Paraholosticha* Kahl, 1932 (for complicated nomenclature of this genus, see Berger 2001). However, species of the *Paraholosticha-Keronopsis* group have many frontal cirri arranged in a corona composed of three fragments, lack a gonostomatid oral apparatus, and divide in

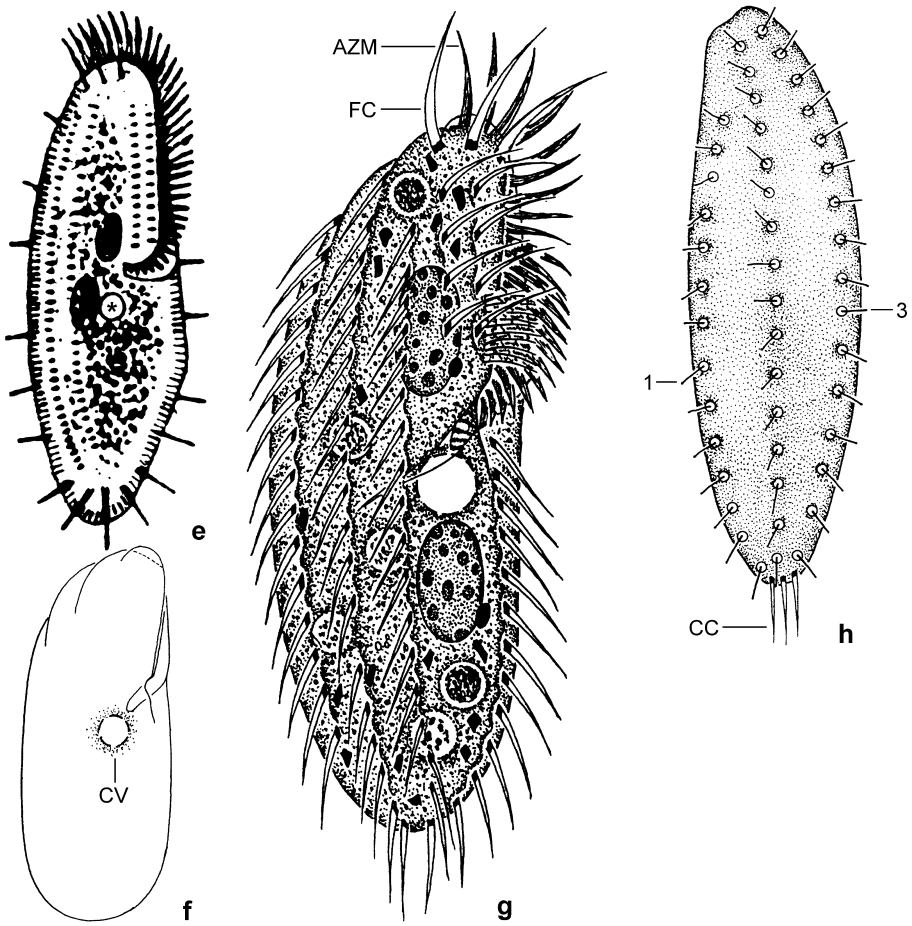


Fig. 40e–h *Wallackia bujoreani* (e, from Lepsi 1951; f–h, from Foissner et al. 2002a. From life). **e:** Ventral view of a representative specimen from the original type locality, 80 µm. Asterisk marks inwards shifted contractile vacuole. **f–h:** Ventral (f, g) and dorsal (h) view of broad (f; 93 µm), representative (g; 75 µm), and slender (h; 80 µm) specimen from Namibian sites. Note deep pits around dorsal bristles (h). AZM = distal end of adoral zone, CC = caudal cirri, CV = inwards shifted contractile vacuole, FC = right frontal cirrus, 1, 3 = dorsal kineties. Page 212.

cysts (e.g., Berger & Foissner 1987, Dieckmann 1988, 1989). Thus, a close relationship of the present species with *Paraholosticha* is unlikely.

In 1989, we found a population very closely resembling the type population of *P. bujoreani* (Berger & Foissner 1989a). Because its somatic and oral ciliature was very similar to that of *Wallackia schiffmanni*, we transferred *P. bujoreani* to this genus. In our comparison with related species we wrote that the extrusomes agree very well. However, Lepsi (1951) described and illustrated rods forming a distinct seam (Fig. 40e), whereas the extrusomes of our population are roughly ellipsoidal form-

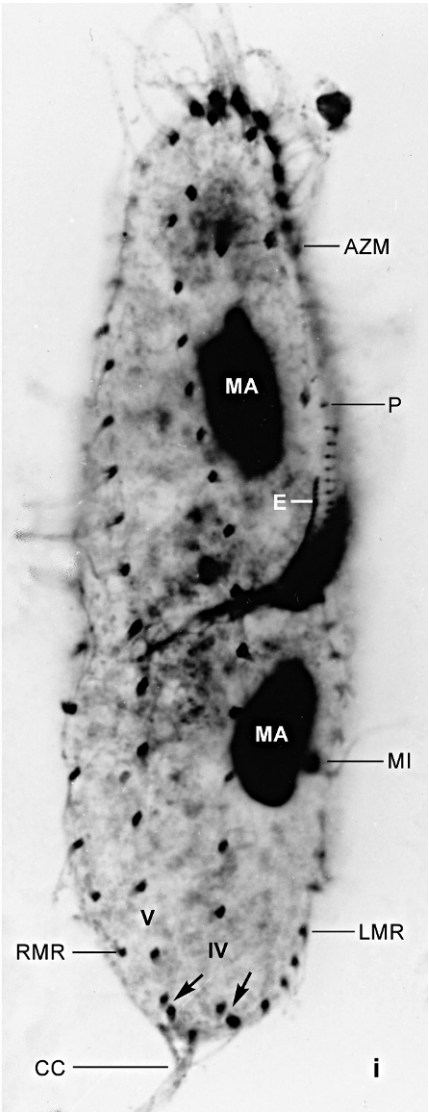


Fig. 40i *Wallackia bujoreani* (from Foissner et al. 2002b. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus. Arrows mark indistinct pretransverse and transverse(?) cirri. Note the gonostomatid oral apparatus, for example, the short paroral which is composed of widely spaced cilia. AZM = adoral zone of membranelles, CC = caudal cirri, E = endoral, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = right marginal row, IV, V = frontoventral rows. Page 212.

ing an indistinct seam (Fig. 40a, b). From *W. schiffmanni* we separated *W. bujoreani* by the habitat, the higher number of cirri in rows II and III, the higher number of dorsal kineties, and the shape and size of the extrusomes. Now I am not so convinced that all these differences apply because (i) *Wallackia schiffmanni* is possibly not a strict limnetic species (rather semiterrestrial); (ii) Lepsi illustrated (Fig. 40e), like Foissner (1976, Fig. 39a), many cirri in cirral rows II and III (however, these data must not be overinterpreted because they are based in both descriptions on live data only); (iii) the number of dorsal kineties was not described by Lepsi (1951) and very likely overestimated by Foissner (1976; see Foissner et al. 2002a, p. 649); and (iv) the extrusomes of *W. schiffmanni* (Fig. 39b) and the population studied by Lepsi (Fig. 40e) are rod-shaped and form a distinct seam. Accordingly, synonymy of *W. bujoreani* and *W. schiffmanni*, already proposed by Hemberger (1982, p. 44), cannot be excluded. Further populations have to be studied to solve the problem finally.

The ventral and dorsal ciliature as well as the morphogenesis of *W. bujoreani* and *Neowallackia franzi* agree rather well, indicating that they are closely related. Major differences exist in the cortical granules (present vs. absent [but also present in *N. ghangriai*]), the number of macronuclear nodules (2 vs. usually 11 or 12), and the caudal cirri (present vs. absent).

Morphology: At first the neotype population from Corsica is described. Additional and/or deviating data of Lepsi's population and an African population (Foissner et al. 2002a) are provided at the end of the morphology section.

Neotype population in life about 70 × 25 µm, that is, body length:width ratio

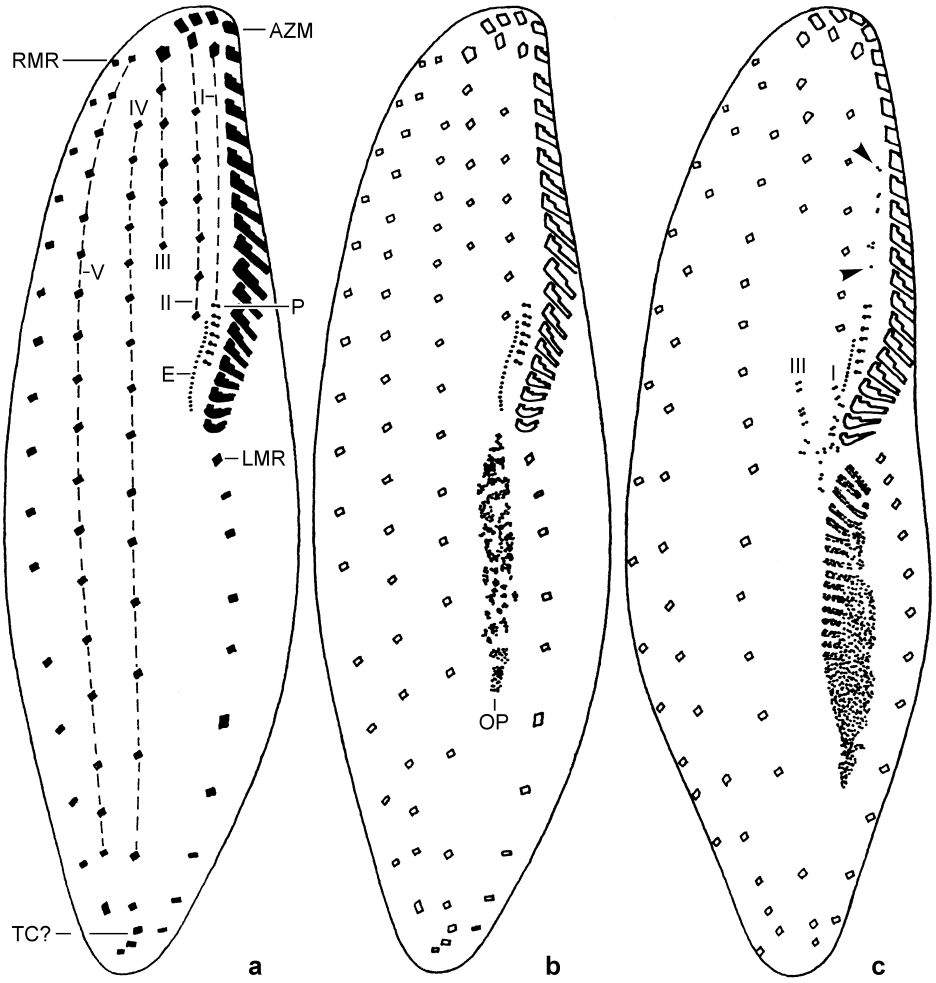


Fig. 41a–c *Wallackia bujoreani* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral side of very early dividers. **a:** Designation of structures; same specimen as (b), but with the oral primordium removed. Cirri originating from same anlage connected by broken line. **b:** The oral primordium originates postorally in the barren area between frontoventral row IV and left marginal row, 70 µm. **c:** Two anlagen are produced from the right anterior end of the oral primordium, where adoral membranelles are forming. Arrowheads mark proter's anlage I, which originates de novo between the adoral zone and the frontoventral row II. AZM = adoral zone of membranelles, E = endoral, LMR = left marginal row, OP = oral primordium, P = paroral, RMR = right marginal row, TC? = transverse cirri (designation as such questionable), I–V = frontoventral cirri rows. Page 212.

about 2.8:1. Body outline elliptical, margins converging anteriad, both ends rounded (Fig. 40a). Macronuclear nodules distinctly left of midline, with small chromatin bodies. Micronuclei closely attached. Contractile vacuole about at 50% of body length, distinctly displaced inwards, and thus at the level of the proximal portion of

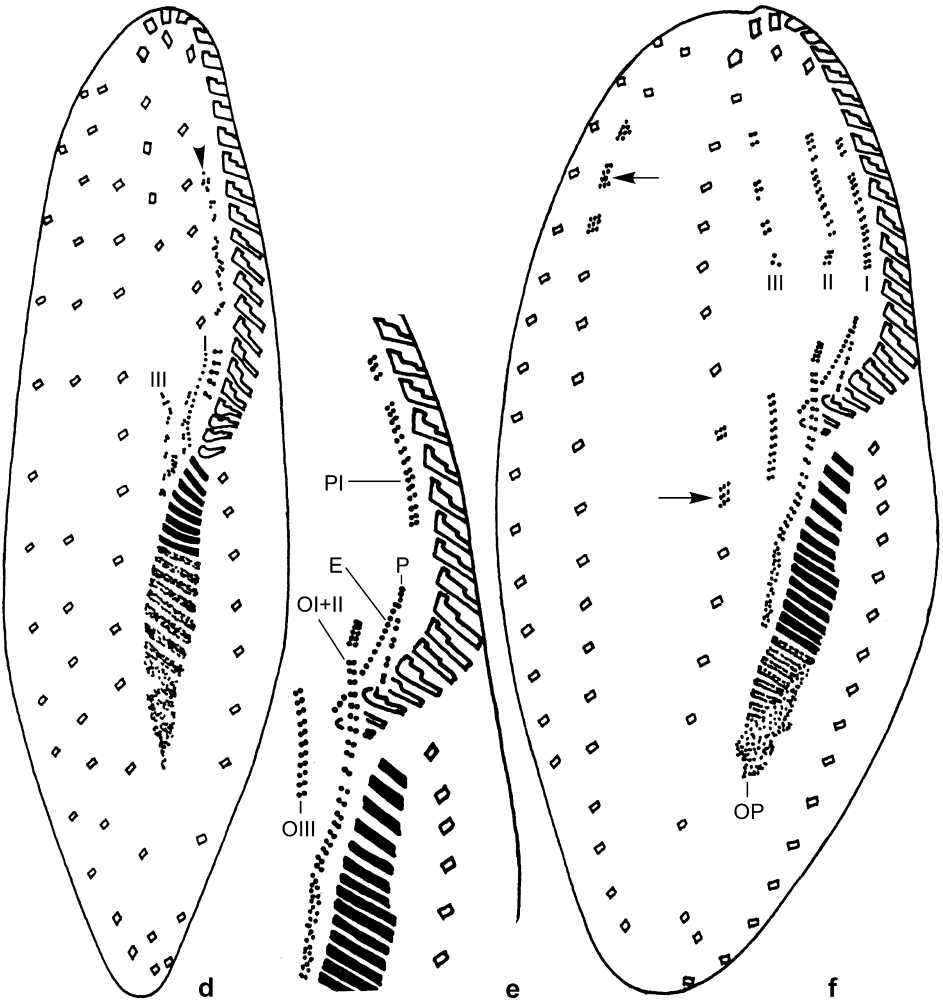


Fig. 41d–f *Wallackia bujoreani* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral side of early dividers. **d:** Specimen similar to that shown in (c), but with more distinct proter anlage I (arrowhead), which obviously originates de novo, a rather unusual mode; 67 µm. **e, f:** The opisthe anlage I develops to a long "primary" primordium right of the oral primordium; 61 µm. The parental cirral rows II and III change to anlagen as a whole (II, III in f), while rows IV and V develop cirral primordia intrakinetally (arrows). E = parental endoral, OP = oral primordium, OI–III = anlagen I–III of opisthe, P = parental paroral, PI = anlage I of proter, I–III = anlagen I–III of proter (f) and opisthe (d; only III indicated). Page 212.

the adoral zone of membranelles (Fig. 40a). Cortical granules (extrusomes) colourless, about 1.5 µm across, ellipsoidal, irregularly arranged; impregnate with protargol (Fig. 40b). Cytoplasm colourless, with some yellowish, about 4 µm large crys-

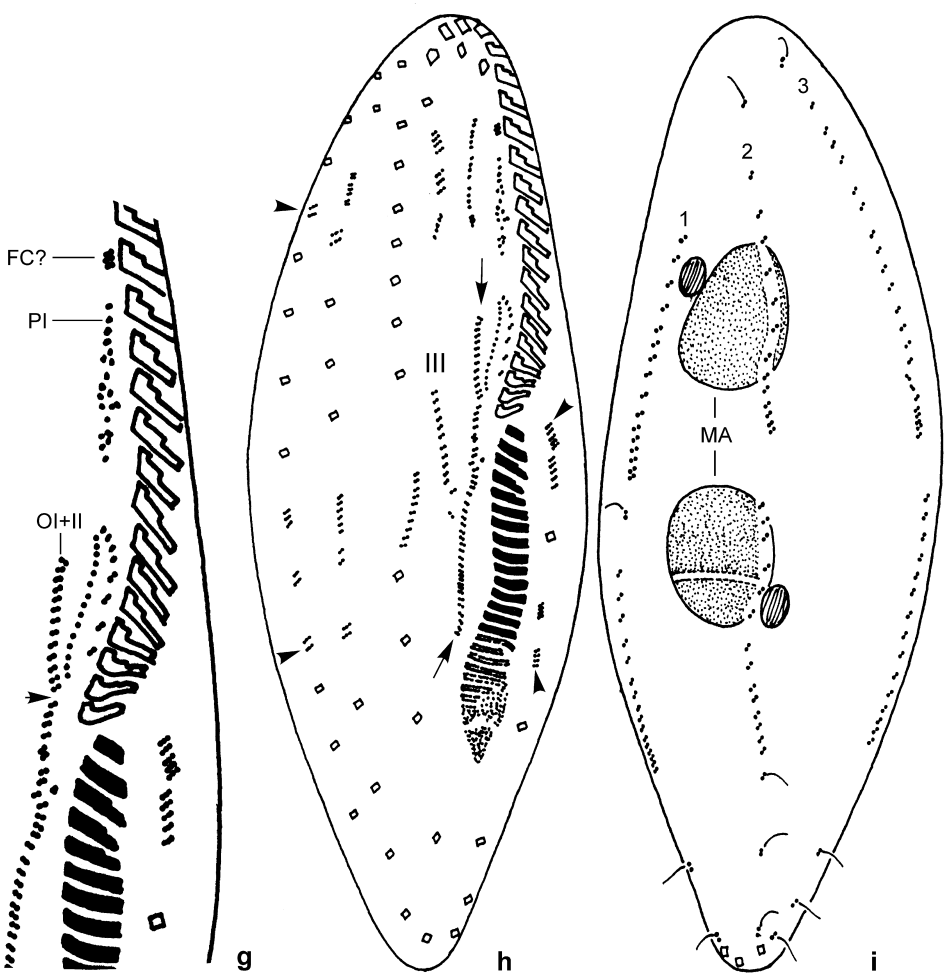


Fig. 41g–i *Wallackia bujoreani* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus of a divider (66 µm) with fully developed opisthe anlage I, which is a very long "primary" primordium (ends marked by long arrows in h) later splitting (short arrow in g) into opisthe's anlagen I and II (j). Arrowheads denote marginal row primordia, which are produced, like the dorsal kinety primordia (i), intrakinetally. FC? = new(?) left frontal cirrus, MA = macronuclear nodules, OI+II = anlagen I and II of opisthe, PI = anlage I of proter, III = anlage III of opisthe, 1–3 = dorsal kineties. Page 212.

tals and some food vacuoles 5–7 µm in diameter (Fig. 40a). Rapid jerky movement, sometimes becoming stationary for a moment.

Oral apparatus *Gonostomum*-like (for details, see p. 15 and Berger 1999), that is, adoral zone commences near midline of anterior body end, extends straight along left body margin, performing abrupt bend and slight clockwise rotation to plunge into buccal cavity near left body margin (Fig. 40a, c); occupies about 50% of body

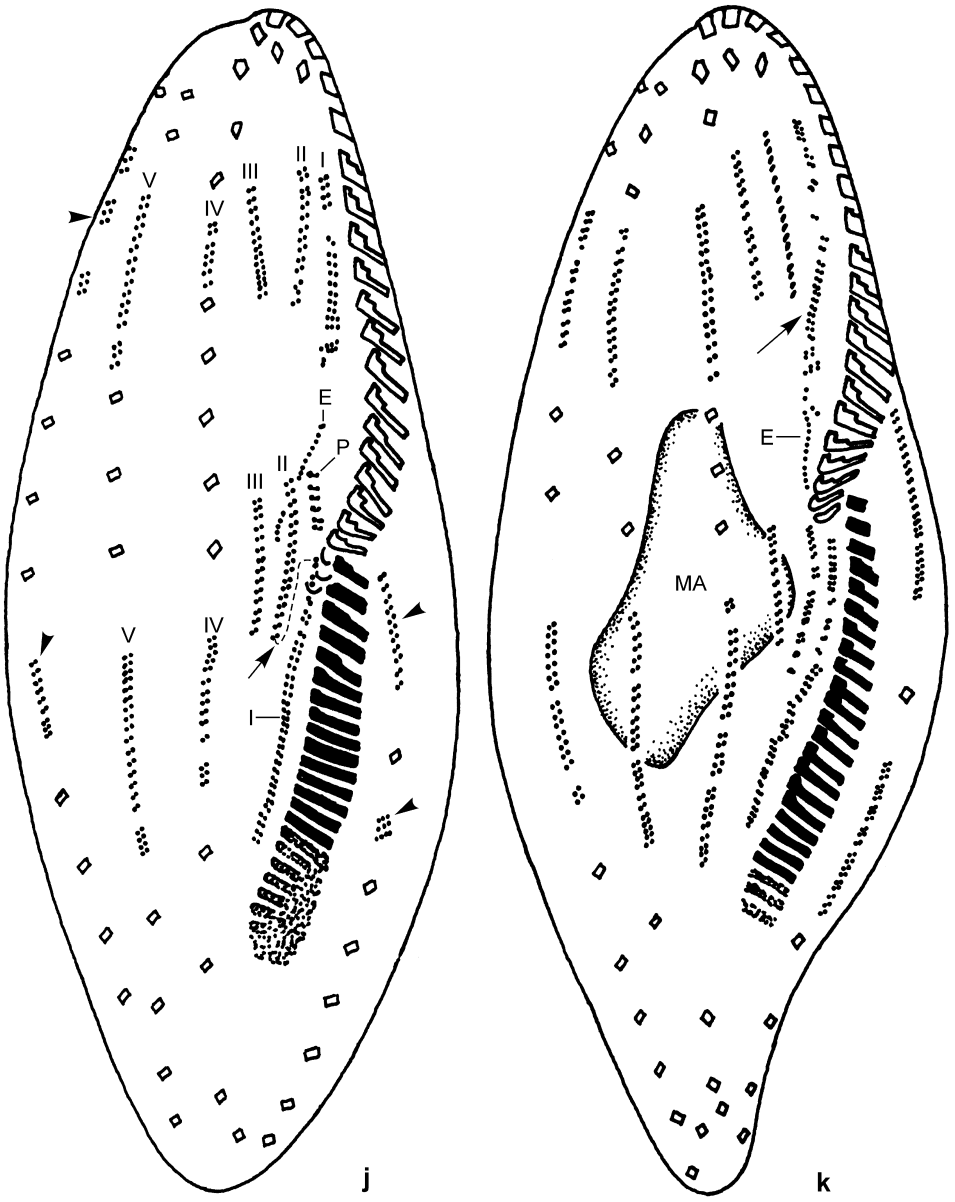


Fig. 41j, k *Wallackia bujoreani* (from Foissner et al. 2002a. Protargol impregnation). Ventral views and nuclear apparatus of middle dividers, j = 60 µm, k = 70 µm. **j:** This divider shows the origin of opisthe's anlage II by transverse splitting of anlage I (arrow marks broken line connecting the fragments), which was an extraordinarily long "primary" primordium (see Fig. 41h). The parental oral apparatus is still almost unchanged, proving that proter's anlage I originated de novo. Arrowheads mark marginal row primordia. All five frontoventral anlagen (I–V) are now recognisable in proter and opisthe. In the proter, they were produced as follows: anlage I originated de novo and produced, as is usual, the left frontal cirrus and the paroral; anlagen II and III originated from parental cirral rows II and III, which changed to cirral primordia as a whole; anlagen IV and V originated intrakinetally from parental cirral rows IV and V. The anlagen of the opisthe originated as follows: anlagen I–III from the oral primordium, whereby anlage II was

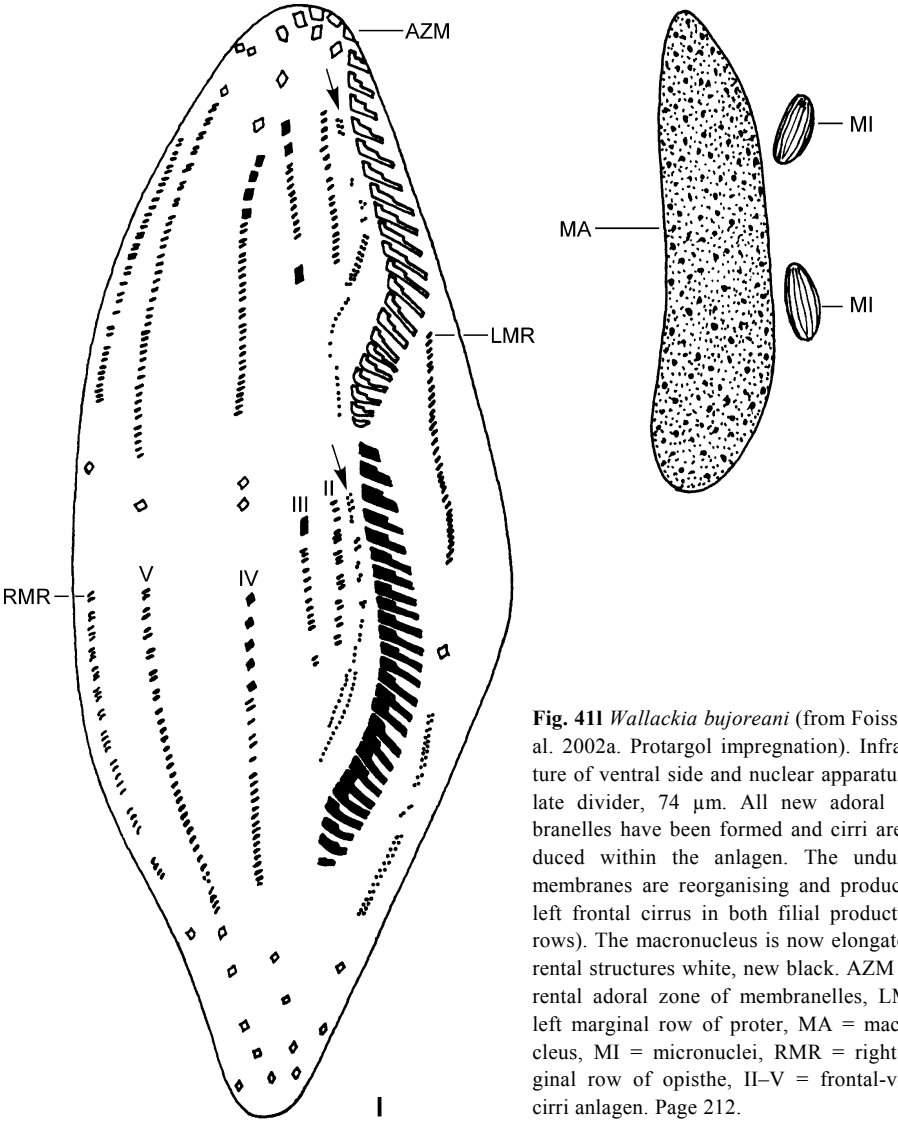


Fig. 411 *Wallackia bujoreani* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus of a late divider, 74 µm. All new adoral membranelles have been formed and cirri are produced within the anlagen. The undulating membranes are reorganising and produce the left frontal cirrus in both filial products (arrows). The macronucleus is now elongate. Parental structures white, new black. AZM = parental adoral zone of membranelles, LMR = left marginal row of proter, MA = macronucleus, MI = micronuclei, RMR = right marginal row of opisthe, II–V = frontal-ventral cirri anlagen. Page 212.

← produced by a fragmentation of a long "primary" primordium. Anlagen IV and V originated intrakinetally from parental cirral rows IV and V. **k:** A middle divider with the two macronuclear nodules fused to a single mass. The parental undulating membranes are reorganising, with the new, de novo-produced paroral ahead (arrow). E = parental endoral, MA = fused macronucleus, P = parental paroral, I–V = frontal-ventral cirral anlagen. Page 212.

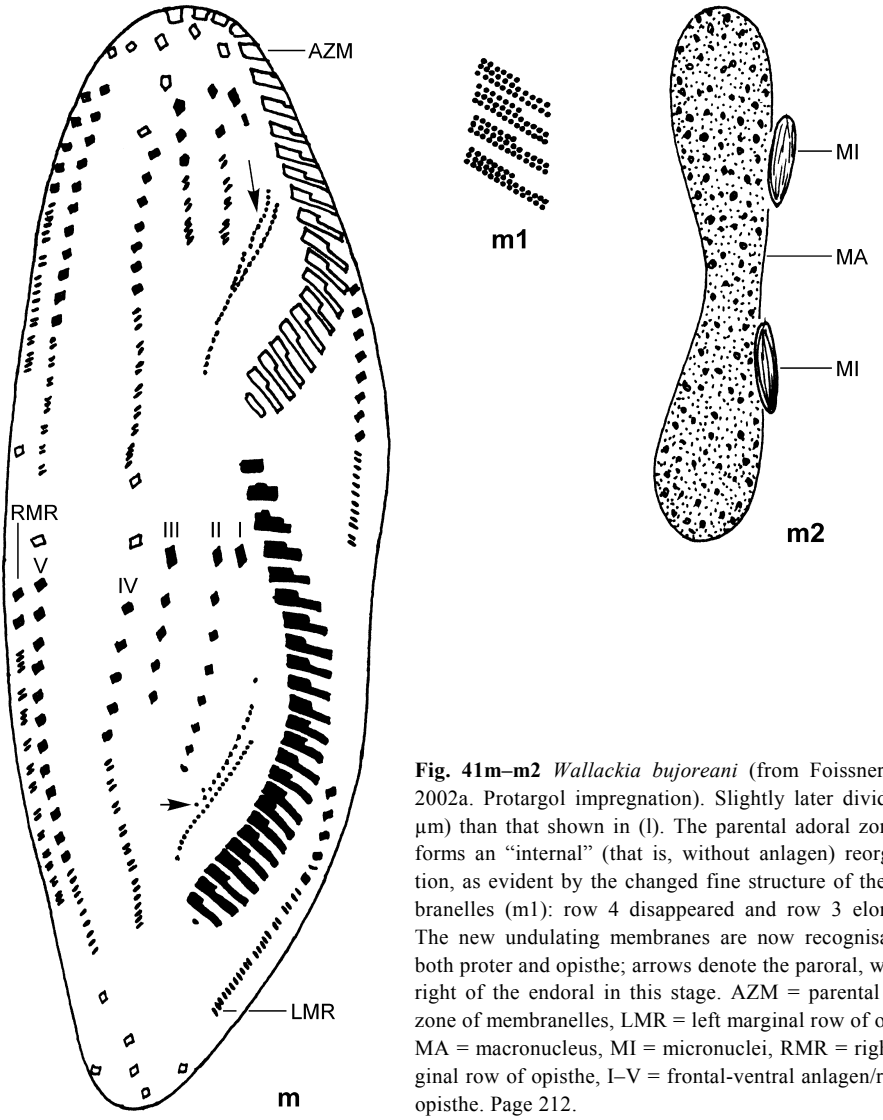


Fig. 41m–m2 *Wallackia bujoreani* (from Foissner et al. 2002a. Protargol impregnation). Slightly later divider (73 µm) than that shown in (l). The parental adoral zone performs an "internal" (that is, without anlagen) reorganisation, as evident by the changed fine structure of the membranelles (m1): row 4 disappeared and row 3 elongated. The new undulating membranes are now recognisable in both proter and opisthe; arrows denote the paroral, which is right of the endoral in this stage. AZM = parental adoral zone of membranelles, LMR = left marginal row of opisthe, MA = macronucleus, MI = micronuclei, RMR = right marginal row of opisthe, I–V = frontal-ventral anlagen/rows of opisthe. Page 212.

length, bases of largest membranelles in life about 4 µm wide. Undulating membranes short, paroral composed of loosely arranged basal bodies (15 in specimen illustrated, Fig. 40c); paroral distinctly ahead of endoral, that is, membranes only slightly optically overlapping.

Cirral pattern and number of cirri of usual variability (Fig. 40c, Table 18). Frontal cirri slightly enlarged, left one distinctly displaced posteriad. Frontoventral rows II and III confined to frontal area, frontoventral row III slightly shorter (ends at 27% of body length in specimen illustrated; Fig. 40c) than row II (ends at 33%). Frontoventral row IV anteriorly slightly shortened (begins at 15% of body length in speci-

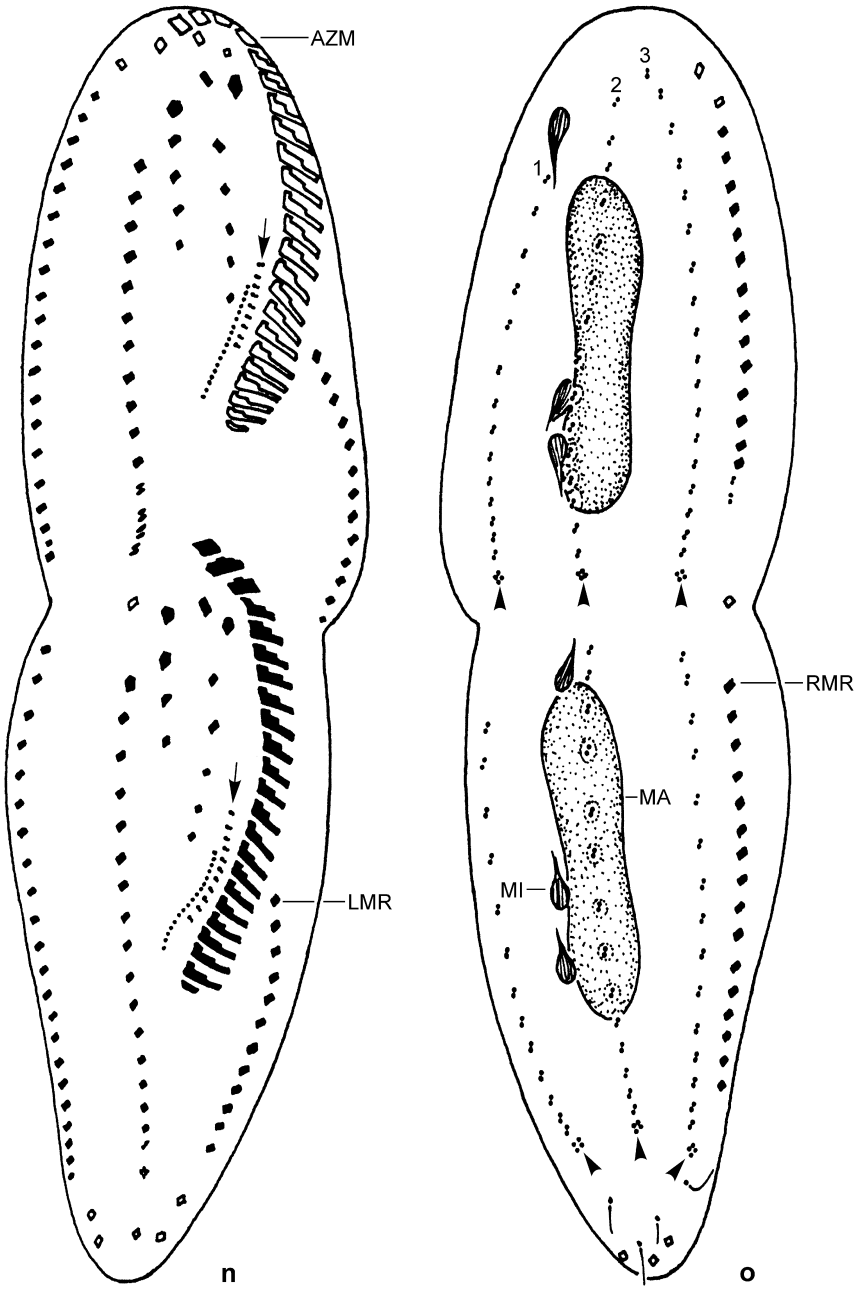
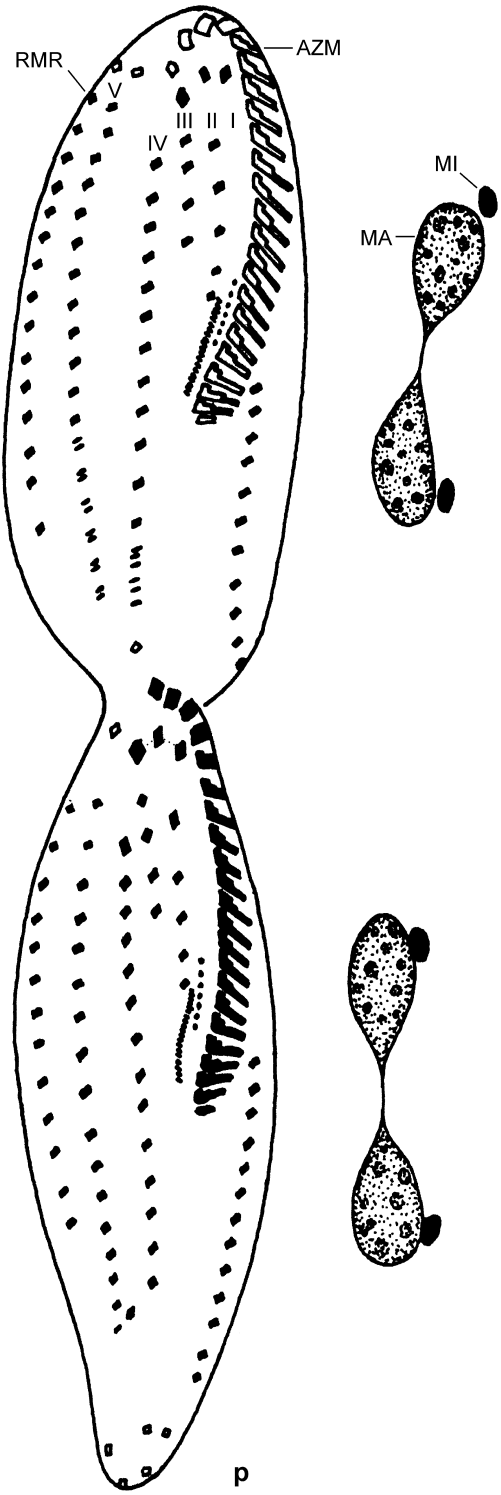


Fig. 41n, o *Wallackia bujoreani* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of a very late divider, 72 µm. Note that the paroral (arrows) is now left of the endoral. The first round of macronuclear and micronuclear division is complete. A caudal cirrus (arrowheads) – composed of four cilia – is formed at the end of each dorsal kinety. Parental structures white, new black. AZM = parental adoral zone, LMR = left marginal row, MA = macronucleus of opisthe, MI = micronucleus, RMR = right marginal, 1–3 = dorsal kineties of proter. Page 212.



men shown in Fig. 40c), terminates – like row V – near rear cell end; row V commences about at level of frontal cirri. Rearmost two cirri of rows IV and V somewhat set off from remaining cirri, that is, possible a pretransverse ventral cirrus and a (basically not enlarged) transverse cirrus is present per row. Right marginal row commences slightly behind level of anterior end of frontoventral row V, ends subterminally; left marginal row begins left of proximal end of adoral zone, terminates near cell end; marginal cirri in life about 12 µm long.

Dorsal bristles about 4 µm long, arranged in three kineties. Kinety 1 more or less distinctly shortened anteriorly; in specimen illustrated it commences at 25% of body length (Fig. 40d) and ends at rear cell end, like kineties 2 and 3, which are not

Fig. 41p *Wallackia bujoreani* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus of a very late divider, 95 µm. Cell elongation and shaping commence. Most cirri not involved in primordia formation have been reduced and the second round of macronuclear division is almost complete. No distinct cirral migration is recognisable, indicating that transverse cirri (sensu stricto) are lacking; however, some migration occurs during final cell-shaping in postdividers because cirral rows IV and V extend to the posterior cell end in the interphase specimens (Fig. 41a). Parental structures white, new black. AZM = parental adoral zone of membranelles, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row of proter, I–V = frontoventral rows. Page 212.

distinctly shortened anteriorly. Caudal cirri narrowly spaced, about 20 µm long in life; one cirrus on each kinety.

Population described by Lepsi (1951; Fig. 40e): Body length:width ratio 2.0 to 2.5:1. Lepsi recognised the cirral pattern very well, although he made only live observations. However, he wrote that transverse and caudal cirri are lacking. Indeed, the transverse cirri are very inconspicuous (if present at all), and Lepsi observed that the marginal cirri are long at the rear end, indicating that he misinterpreted (due to the lack of silver impregnation) the caudal cirri as marginal cirri. He even described and illustrated the distinctly inwards shifted contractile vacuole (Fig. 40e). The sole remarkable difference is in the shape of the cortical granules (extrusomes), which he described and illustrated as short, straight rods (Fig. 40e). By contrast, they are roughly globular in the neotype population (Fig. 40b). The rod-shape is reminiscent of *W. schiffmanni* (see remarks).

Additional observations on Namibian population studied by Foissner et al. (2002a; Fig. 40f–i): Shape highly variable (Fig. 40f–g) and indistinguishable from that of *Gonostomum affine* (for review of this species, see p. 68 and Berger 1999, p. 369). Cortex glassy and distinctly crenelated along cirral rows; dorsal bristles, as in neotype population, 4 µm long and originating in conspicuous pits (vacuoles?) about 2 µm across (Fig. 40h). Both features (glassy cortex and pits) are very likely caused by the highly saline environment, as indicated by the dorsal bristles, which appear as is usual in protargol preparations. Due to the glassy cortex, the cortical granules – although rather large – are almost invisible in life specimens. Fortunately, they impregnate strongly with protargol. However, in specimens from the non-saline Namibian site (49), they do not impregnate, but stand out as white rods from the brownish cytoplasm. Food vacuoles 4–5 µm across. Cilia of paroral and most cirri about 10 µm long in life, frontal and caudal cirri about 15 µm long. Paroral of specimen (very early divider) illustrated in Fig. 41b composed of only seven kinetids[1]. Transverse cirri as indistinct as in neotype population. No elongated dorsal bristles at posterior body end, an important difference to *W. schiffmanni* (Fig. 40g, h vs. Fig. 39d, arrows).

Cell division (Fig. 41a–p): This part of the life cycle was studied by Foissner et al. (2002a) in specimens from the Namibian site (54). Morphogenesis commences with the de novo formation (that is, no parental cirri involved) of an oral primordium in the barren postoral area between the left marginal row and the frontoventral row IV (Fig. 41b). In the next phase, adoral membranelles develop within the oral primordium from anterior to posterior and two primordia originate from the right anterior end of the oral primordium; these anlagen, which consist of few dikinetids, extend up to the level of the parental paroral. The left primordium is opisthe's anlage I, while the right is anlage III; anlage II of the opisthe is later produced from anlage I, which transforms into a long "primary" primordium. Simultaneously, scattered basal bodies appear between the mid-portion of the adoral zone and frontoventral row II.

[1] It is not known why the kinetids of this population look like dikinetids (parasomal sac or base of cilia impregnated?).

These basal bodies contact neither parental cirri nor undulating membranes, that is, they develop de novo (Fig. 41c). Their number increases rapidly to form a conspicuous anlage, which organises to a long row of oblique kinetids becoming proter's anlage I (Fig. 41d–f).

The next ontogenetic stage is characterised by the formation of primordia in frontoventral rows II and III, which change as a whole to dikinetidal anlagen streaks, and rows IV and V, which begin anlagen formation subequatorially and near anterior end, respectively. In addition, the two primordia produced by the oral primordium modify to distinct, dikinetidal streaks, of which the left is a very long "primary" primordium extending into the proter oral area. Membranelle formation is almost complete in the oral primordium, and the parental oral structures appear unchanged (Fig. 41e, f), although the oral area flattens and thus slightly dislocates the undulating membranes (Fig. 41g, h). The de novo-produced proter anlage I forms, as is usual, the left frontal cirrus at its anterior end. Between this and the next stage (Fig. 41j), the very long primordium (anlage I) of the opisthe splits: the anterior third becomes opisthe's anlage II, while the posterior portion will produce the opisthe's undulating membranes and left frontal cirrus (Fig. 41g, h, j, l).

In early to middle dividers, all cirral anlagen are recognisable, while the parental undulating membranes are still unchanged (Fig. 41j). The anlagen of the proter are formed as follows: anlage I de novo; anlagen II and III develop from parental cirral rows II and III, which change to cirral primordia as a whole; anlagen IV and V originate intrakinetally in cirral rows IV and V. The anlagen of the opisthe are formed differently: anlagen I and III develop from the oral primordium, whereas anlage II is produced from a primordium which splits transversely[1] (the anterior portion becomes anlage II, the rear portion becomes anlage I); anlagen IV and V are formed intrakinetally in the parental rows IV and V.

In middle stages, the parental undulating membranes disorganise. Most cirri are modified to anlagen, leaving only a few parental cirri each at anterior and posterior end of the frontoventral cirral rows and in mid body (Fig. 41k). Next, cirri are formed within the anlagen, and the undulating membrane anlage of the opisthe splits longitudinally to form the paroral (right row in Fig. 41l) and the left frontal cirrus (= cirrus I/1). In the proter, the new undulating membranes begin to organise: the endoral very likely develops from parental basal bodies, while the paroral originates from the posterior part of anlage I, whose anterior portion produces the left frontal cirrus. Finally, two rows of slightly scattered basal bodies are recognisable in both filial products; the left row becomes the endoral, the right the paroral (Fig. 41l, m).

Late and very late cell division stages (Fig. 41m–p) show few peculiarities, except for two features, namely, (i) the parental adoral zone reorganises internally because the membranelles lose basal body row 4 and increase length of row 3 (Fig.

[1] In the original paper (Foissner et al. 2002a, p. 637, footnote 27) we discussed that a new term should possibly be created because this "primary primordium" (a term introduced by Foissner 1983a) does not produce an anlagen streak each for proter and opisthe, as is usual, but both parts remain in the opisthe.

41m1); and (ii) the paroral migrates to the ventral surface[1], that is, underneath the endoral so that the left row is now the paroral and the right the endoral (Fig. 41m, n). True transverse cirri are not recognisable; only the rearmost two cirri of rows IV and V are somewhat set off (Fig. 41a, n, p).

Anlagen appear intrakinetally in the marginal rows and dorsal kineties at two levels (Fig. 41h–j). A caudal cirrus is formed at the end of each dorsal kinety (Fig. 41o). In middle stages, the macronuclear nodules fuse to a globular mass (Fig. 41k). Later, this mass divides to the species-specific number of two nodules (Fig. 41m2, o, p).

Occurrence and ecology: Very likely *W. bujoreani* is confined to terrestrial habitats. Records are only known from the Holarctis and the Palaeotropis (Foissner 1998, Foissner et al. 2002a, p. 56). Lepsi (1951) discovered it in arable soil from near the village Timisoara, Romania. Due to the neotypification, the type locality is now the sample site of the neotype population, namely, the bank of a small river (500–600 m above seal level) near the reservoir Ajaccio, Corsica, France; we found it there in a sandy, brown soil (pH 4.1) with litter of grass, about 10 m away from the river (Berger & Foissner 1989a). In Namibia, *Wallackia bujoreani* occurred at saline sites (up to 20‰; for detailed descriptions of sites 54, 59, 60, 71, see Foissner et al. 2002a), having pH values between 8 and 9, but also in a non-saline sample from site (49). These records show that *W. bujoreani* is euryhaline and possibly cosmopolitan, inhabiting such different biotopes as arable soils and saline steppes (Foissner et al. 2002a). Petz et al. (2007, p. 401) recorded it from freshwater in the High Arctic.

Wallackia bujoreani feeds on bacteria (Berger & Foissner 1989a, Foissner et al. 2002a). Biomass of 10^6 specimens about 15 mg (Foissner 1998, p. 211).

Wallackia elegans Foissner, Agatha & Berger, 2002
(Fig. 42a–l, Table 18)

2002 ***Wallackia elegans* nov. spec.**[2] – Foissner, Agatha & Berger, Denisia, 5: 643, Fig. 144a–h, j–l, 381r, Table 126 (Fig. 42a–l; original description; the holotype slide [accession number 2002/375; see Aescht 2008, p. 153], two paratype slides [2002/343, 376], and three voucher slides [2002/377–379] have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria).

Nomenclature: The Latin adjective *elegans* (elegant, dainty) refers to the elegant appearance of the species (Foissner et al. 2002a, p. 643).

[1] In the original paper (Foissner et al. 2002a, p. 637) we wrote that the paroral moves over the endoral.

[2] Foissner et al. (2002a) provided the following diagnosis: Size about 60 × 17 µm in vivo. Lanceolate with narrowed posterior portion curved rightwards. Two closely spaced macronuclear nodules. On average 3 buccal cirri, 3 cirri in frontoventral row three, 6 cirri in frontoventral row four, 17 cirri in frontoventral row five, and 3 transverse cirri. Caudal cirri 1/3–1/2 of body length and thus very prominent. Adoral zone about 46% of body length, composed of 19 membranelles on average. Usually 10 paroral kinetids.

Table 18 Morphometric data on *Wallackia bujoreani* (buj, from Berger & Foissner 1989a) and *Wallackia elegans* (el1, type population from Namibia; el2, Tenerife population; both from Foissner et al. 2002a, b)

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	buj	67.4	67.0	7.7	2.3	11.4	52.0	80.0	11
	el1	53.0	53.0	4.4	1.0	8.3	44.0	62.0	21
	el2	52.3	52.0	6.0	1.8	11.4	42.0	62.0	11
Body, width	buj	24.4	22.0	5.1	1.5	20.8	17.0	36.0	11
	el1	16.0	16.0	1.8	0.4	11.0	14.0	19.0	21
	el2	12.5	13.0	1.7	0.5	13.6	9.0	15.0	11
Body length:width, ratio	el1	3.3	3.3	0.3	0.1	8.1	2.8	3.7	21
	el2	4.3	4.1	0.7	0.2	16.1	3.3	6.0	11
Adoral zone of membranelles, length	buj	33.8	35.0	3.3	1.0	9.6	25.0	36.0	11
	el1	24.4	25.0	1.7	0.4	6.9	22.0	27.0	21
	el2	21.1	21.0	2.1	0.6	9.8	18.0	26.0	11
Body length:length of adoral zone, ratio	el1	2.2	2.1	0.2	0.1	10.1	1.8	2.6	21
	el2	2.5	2.4	0.3	0.1	10.3	2.1	3.1	11
Anterior body end to paroral, distance	el1	14.4	14.0	1.8	0.4	12.3	11.0	18.0	21
Paroral, length	el1	6.6	6.0	0.9	0.2	14.4	5.0	8.0	20
Anterior body end to endoral, distance	el1	16.8	17.0	1.3	0.3	8.0	14.0	19.0	21
Endoral, length	el1	7.6	8.0	0.9	0.2	11.5	6.0	9.0	21
Anterior body end to posterior end of frontoventral row III, distance	el1	11.2	11.0	2.6	0.6	22.9	8.0	17.0	21
	el2	7.7	7.0	2.1	0.6	27.8	5.0	12.0	11
Anterior body end to posterior end of frontoventral row IV, distance	el1	20.5	21.0	3.1	0.7	15.1	14.0	25.0	21
	el2	18.4	18.0	3.0	0.9	16.2	15.0	24.0	11
Anterior body end to posterior end of frontoventral row V, distance	el1	48.4	48.0	4.8	1.1	10.0	40.0	60.0	21
	el2	50.7	50.0	5.9	1.8	11.6	40.0	60.0	11
Anterior body end to right marginal row, distance	el1	4.9	5.0	1.1	0.2	23.2	3.0	7.0	21
Posterior body end to right marginal row, distance	el1	11.6	10.0	5.8	1.3	50.3	4.0	26.0	21
Anterior body end to anterior macronuclear nodule, distance	el1	10.8	11.0	1.1	0.2	10.0	9.0	13.0	21
Nuclear figure, length	el1	22.6	23.0	2.0	0.4	8.9	18.0	26.0	21
Macronuclear nodules, distance in between	el1	2.6	2.5	0.9	0.2	36.1	1.0	4.0	21
Anterior macronuclear nodule, length	el1	10.4	10.0	1.0	0.2	9.4	9.0	13.0	21
	el2	9.3	9.0	1.4	0.4	15.3	7.0	11.0	11
Anterior macronuclear nodule, width	el1	4.4	4.0	0.7	0.1	15.3	3.0	6.0	21
	el2	4.2	4.0	0.6	0.2	14.4	3.0	5.0	11
Posterior macronuclear nodule, length	buj	12.4	12.0	2.0	0.6	16.3	10.0	17.0	11
Posterior macronuclear nodule, width	buj	4.7	4.0	1.0	0.3	21.3	4.0	7.0	11
Macronuclear nodules, number	buj	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	el1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	el2	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Anterior micronucleus, length	el1	2.0	2.0	–	–	–	1.5	2.5	21
	el2	2.1	2.0	–	–	–	2.0	2.2	11
Anterior micronucleus, width	el1	1.7	1.5	–	–	–	1.5	2.0	21
	el2	1.7	1.6	–	–	–	1.4	2.2	11
Posterior micronucleus, length	buj	2.6	3.0	0.5	0.2	20.3	1.8	3.0	11
Posterior micronucleus, width	buj	1.4	1.5	0.3	0.1	21.4	1.0	2.0	11
Micronuclei, number	buj	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	el1	2.0	2.0	0.3	0.1	15.8	1.0	3.0	21
	el2	2.1	2.0	–	–	–	2.0	3.0	11

Table 18 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Adoral membranelles, number	buj	25.3	25.0	1.4	0.4	5.3	23.0	27.0	11
	el1	18.7	19.0	1.0	0.2	5.1	17.0	20.0	21
	el2	16.9	16.0	1.1	0.3	6.7	16.0	19.0	11
Paroral, number of cilia	el1	9.5	9.5	1.1	0.2	11.1	8.0	11.0	20
	el2	7.6	7.0	1.2	0.4	16.4	6.0	10.0	9
Frontal cirri, number	buj	3.0	3.0	0.0	0.0	0.0	3.0	3.0	9
	el1 [d]	3.0	3.0	–	–	–	2.0	4.0	21
	el2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
Buccal row (= frontoventral row II), number of cirri [f]	buj	2.2	2.0	0.4	0.1	19.2	2.0	3.0	10
	el1	2.8	3.0	0.9	0.2	34.2	2.0	5.0	21
	el2	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Frontoventral row III, number of cirri [f]	buj	3.0	3.0	0.5	0.1	15.7	2.0	4.0	10
	el1	2.9	3.0	0.9	0.2	31.9	2.0	5.0	21
	el2	2.1	2.0	–	–	–	2.0	3.0	11
Frontoventral row IV, number of cirri	buj	11.8	12.0	1.4	0.4	11.9	10.0	14.0	11
	el1	5.7	6.0	0.7	0.2	12.5	5.0	7.0	21
	el2	5.5	5.0	0.8	0.2	15.0	5.0	7.0	11
Frontoventral row V, number of cirri	buj	13.2	13.0	1.3	0.4	9.5	11.0	15.0	11
	el1	17.1	17.0	2.5	0.5	14.7	12.0	22.0	21
	el2 [b]	16.5	16.0	2.0	0.6	12.3	14.0	21.0	11
"Transverse" cirri, number	el1 [c]	2.5	3.0	1.2	0.3	49.4	0.0	5.0	21
Right marginal cirri, number	buj	10.5	10.5	1.1	0.3	10.3	9.0	12.0	10
	el1	13.4	13.0	3.9	0.9	29.4	8.0	23.0	21
	el2	11.2	11.0	1.4	0.4	12.5	9.0	14.0	11
Left marginal cirri, number	buj	8.9	9.0	0.8	0.3	9.3	8.0	10.0	11
	el1	13.0	13.0	1.9	0.4	14.8	9.0	17.0	21
	el2	10.9	11.0	1.2	0.4	11.2	9.0	13.0	11
Caudal cirri, number	buj	3.0	3.0	0.0	0.0	0.0	3.0	3.0	7
	el1 [e]	3.0	3.0	–	–	–	3.0	4.0	20
	el2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Dorsal kineties, number	buj	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	el1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	el2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Dorsal kinety 1, number of bristles	el1	10.6	11.0	1.7	0.4	16.3	7.0	13.0	20
Dorsal kinety 2, number of bristles	el1	11.7	12.0	1.6	0.4	13.4	9.0	14.0	20
Dorsal kinety 3, number of bristles	el1	13.0	13.0	1.4	0.3	10.6	11.0	16.0	20

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] In Tenerife specimens, "transverse" cirri included.

[c] In the type population (el1), cirri not in line with frontoventral row V and/or the marginal rows were counted as "transverse" cirri. In the population from Tenerife, these were include in frontoventral row V.

[d] Of 21 specimens analysed from the type population, two had two, and one had four frontal cirri.

[e] Of 20 specimens analysed from the type population, two had four caudal cirri.

[f] Frontal cirrus not included.

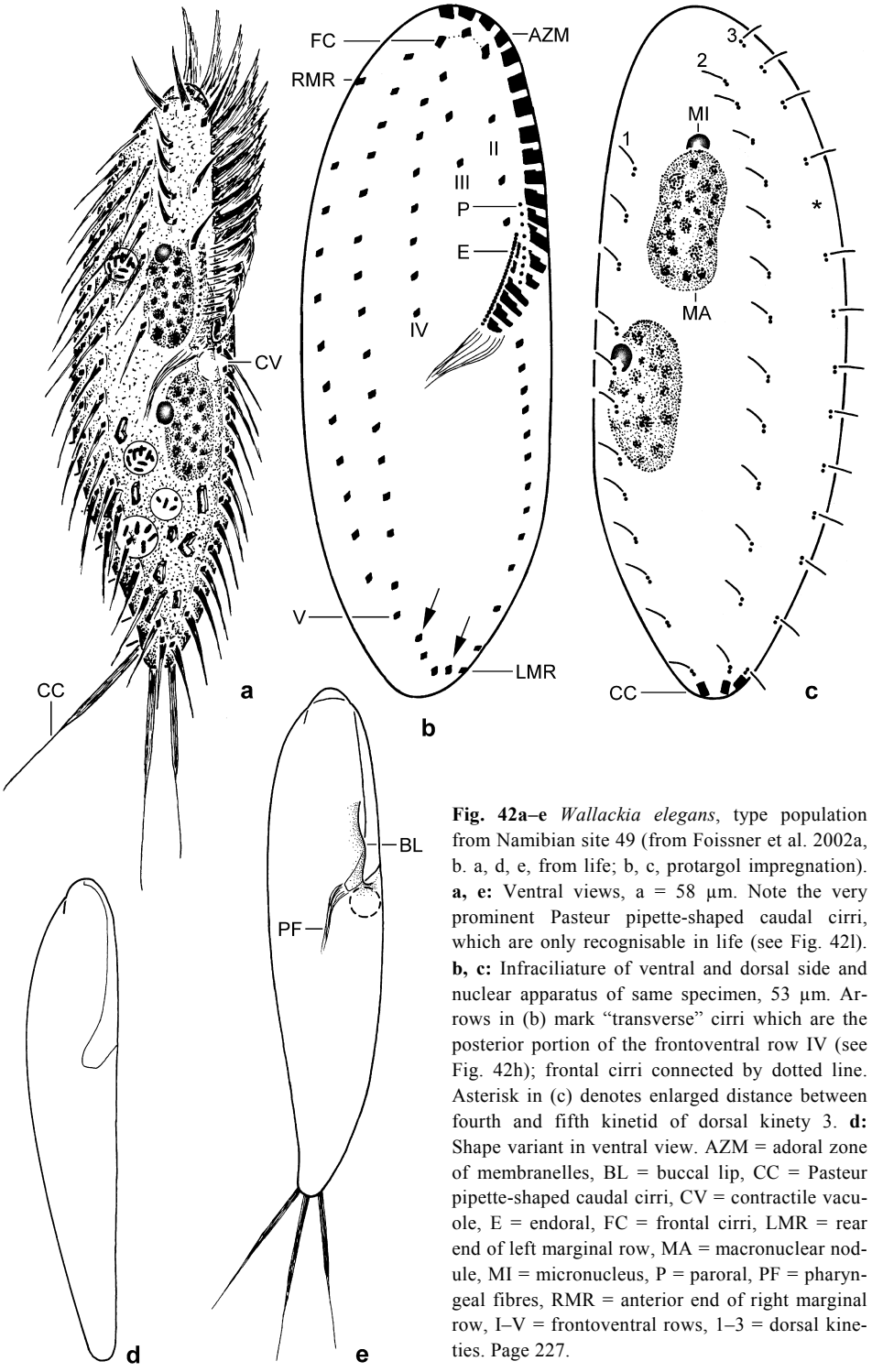


Fig. 42a–e *Wallackia elegans*, type population from Namibian site 49 (from Foissner et al. 2002a, b. a, d, e, from life; b, c, protargol impregnation). **a, e:** Ventral views, a = 58 µm. Note the very prominent Pasteur pipette-shaped caudal cirri, which are only recognisable in life (see Fig. 42l). **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 53 µm. Arrows in (b) mark "transverse" cirri which are the posterior portion of the frontoventral row IV (see Fig. 42h); frontal cirri connected by dotted line. Asterisk in (c) denotes enlarged distance between fourth and fifth kinetid of dorsal kinety 3. **d:** Shape variant in ventral view. AZM = adoral zone of membranelles, BL = buccal lip, CC = Pasteur pipette-shaped caudal cirri, CV = contractile vacuole, E = endoral, FC = frontal cirri, LMR = rear end of left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = anterior end of right marginal row, I–V = frontoventral rows, 1–3 = dorsal kineties. Page 227.

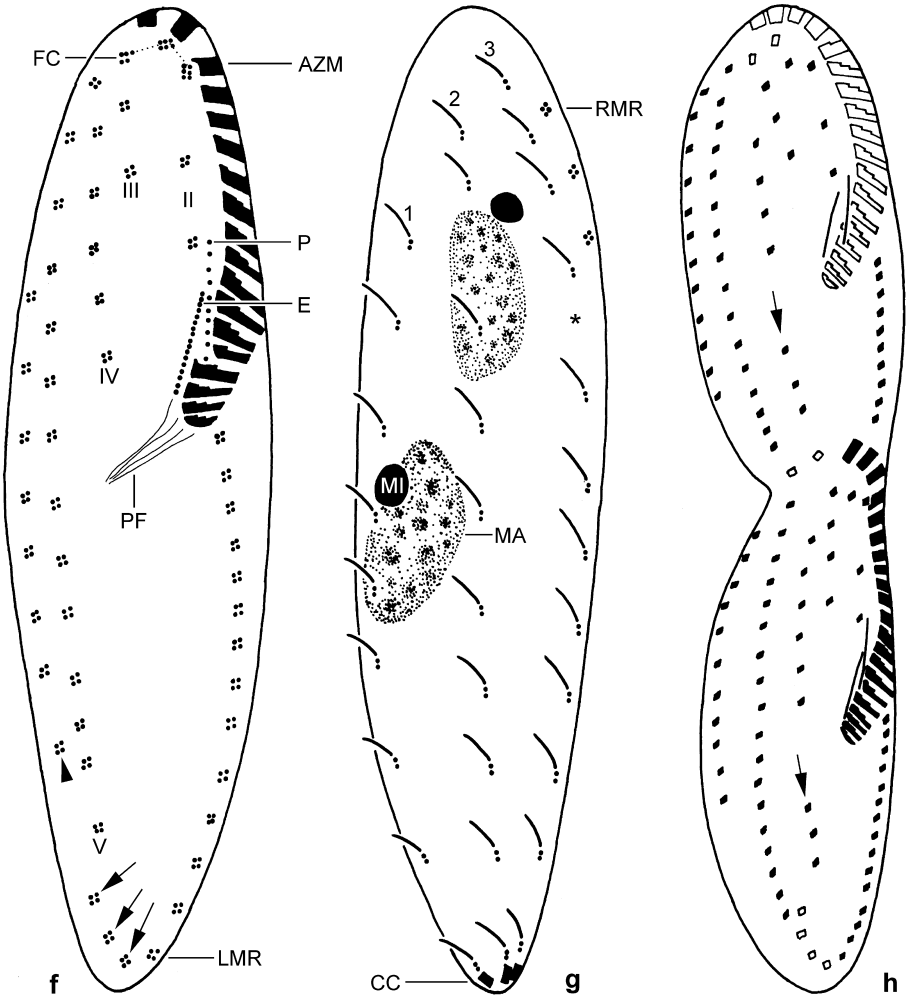


Fig. 42f–h *Wallackia elegans*, type population (from Foissner et al. 2002a, b. Protargol impregnation). **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 57 µm. Arrowhead marks rear end of right marginal row, arrows denote "transverse" cirri. Asterisk in (g) marks enlarged distance between fourth and fifth kinetid of dorsal kinety 3; likely this is a specific feature of *W. elegans* because it also occurs in the Tenerife population (Fig. 42k). **h:** Ventral side of late divider showing that the posterior portion of frontoventral row IV migrates posteriad forming the "transverse" cirri (arrows). AZM = adoral zone of membranelles, CC = caudal cirri, E = endoral, FC = frontal cirri, LMR = rear end of left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = anterior end of right marginal row, I–V = frontoventral rows, 1–3 = dorsal kineties. Page 227.

Remarks: Wilhelm Foissner knew this *Gonostomum*-like species with conspicuous caudal cirri for many years. According to the gonostomatid oral apparatus, the three dorsal kineties, and the caudal cirri, it could be assigned to *Gonostomum* (p. 58) or *Wallackia*. However, according to the cirral pattern, it unequivocally belongs

to *Wallackia*. The pattern closely resembles that of *W. schiffmanni* and *W. bujoreani* because it is composed of five (row I included) frontoventral rows, including a distinct buccal row (= row II). Some dividers show that only five frontal-ventral primordia are formed. In addition, *Wallackia elegans* has – like the type species – prominent, Pasteur pipette-shaped caudal cirri, a feature only recognisable in live specimens. By contrast, *Gonostomum* species have a single buccal cirrus and more or less distinctly scattered frontal-ventral-transverse cirri which can be – at least in some species (e.g., *G. affine*, *G. kuehnelti*) – easily homologised with that of the 18-cirri hypotrichs. Further, both in most 18-cirri hypotrichs and in *Gonostomum*, the frontal-ventral-transverse cirri originate from six anlagen and the caudal cirri are inconspicuous in *Gonostomum* (vs. from five anlagen and distinct in *Wallackia*; for details on *Gonostomum*, see Berger 1999 and p. 58). *Neowallackia* also forms its frontal-ventral cirri from five anlagen, but lacks caudal cirri (p. 280).

The present species is easily distinguished from *W. schiffmanni* and *W. bujoreani* by the body shape (lanceolate with short tail curved to right vs. ellipsoidal), the relative length of the caudal cirri, and the lack of cortical granules. Furthermore, it differs from the limnetic *W. schiffmanni* by body length (50–70 µm vs. 85–100 µm) and the lower number of cirri in the frontoventral rows II to IV (2–5, 2–5, 5–7 vs. 5–7, 5–7, 13). In *W. bujoreani*, frontoventral row IV is composed of 10–14 cirri and terminates near the rear cell end (vs. 5–7 cirri and near buccal vertex in *W. elegans*).

Gonostomum gonostomoidum (Hemberger, 1985) Berger, 1999 has, like the present species, a long frontoventral row left of the right marginal row (Fig. 25a). However, this species – discovered in an infusion of excrement from the terrestrial snail *Deroceras reticulatum* – is 110–200 µm long, has only one buccal cirrus, and forms six frontal-ventral-transverse cirri primordia. Thus, its classification in *Gonostomum* seems correct. *Paragonostomum* species have a similar habitus, but a different cirral pattern (p. 172).

In life, *Wallackia elegans* is characterised by the following combination of features (Foissner et al. 2002a): body 50–70 µm long; lanceolate with rear portion curved to right and bearing very long, prominent caudal cirri; many ventral cirri in several distinct rows

Morphology: The description of the type population is rather comprehensive. Some additional data from a second population are provided in the last paragraph of the morphology section.

Body size of type population 50–70 × 15–20 µm in life; length:width ratio usually 3–4:1 in life and after protargol impregnation (Table 18). Body outline lanceolate to elongate elliptical with narrowed posterior portion usually curved rightwards; right margin thus often slightly sigmoidal and left one convex. Body dorsoventrally flattened up to 2:1; acontractile, but flexible and fragile, narrowed end thus usually not recognisable in prepared specimens (Fig. 42a–g). Macronuclear nodules unusually arranged, that is, closely spaced with posterior nodule very near to left cell margin (Fig. 42a, c, g); individual nodules ellipsoidal to elongate ellipsoidal, contain numerous globular chromatin bodies. Micronuclei usually attached to macronuclear

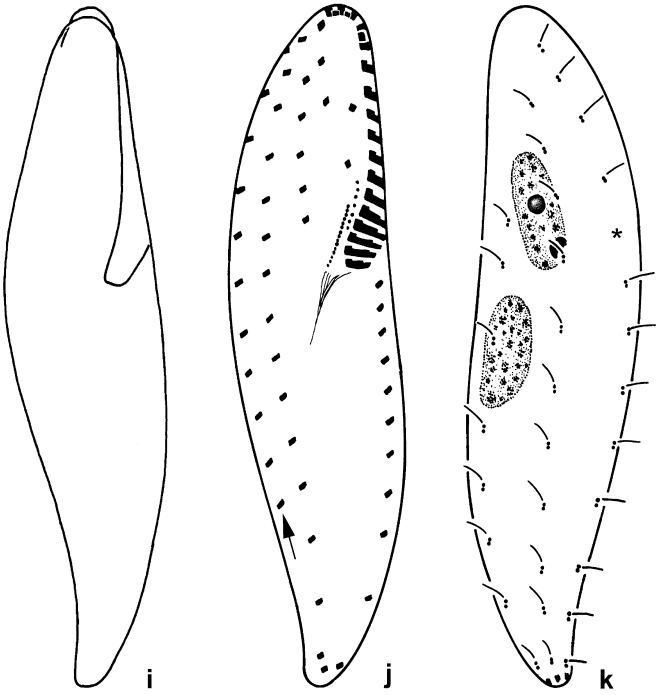


Fig. 42i–k *Wallackia elegans*, Tenerife population (from Foissner et al. 2002a, b. i, from life; j, k, protargol impregnation). **i:** Shape variant in ventral view. **j, k:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 55 µm. Arrow denotes rear end of right marginal row. Asterisk in (k) marks enlarged distance between fourth and fifth kinetid of dorsal kinety 3. For a more detailed labelling, see Fig. 42b, c, f, g. Page 227.

nodules, globular. Contractile vacuole behind buccal vertex at left cell margin, during diastole without distinct collecting canals (Fig. 42a). No cortical granules. Cytoplasm colourless, contains some yellowish, 1–3 µm-sized, highly refractive crystals mainly in rear body portion. Food vacuoles 3–5 µm across. Glides rather rapidly on microscope slide, occasionally resting for a few seconds.

Oral apparatus in *Gonostomum*-pattern (Fig. 42a, b, d–f, Table 18; for explanation see p. 15 and Berger 1999). Adoral zone occupies 38–54%, on average 46% of body length, composed of an average of 19 membranelles, commences near midline of anterior body end, extends straight along left body margin, performing abrupt bend and slight clockwise rotation to plunge into buccal cavity near left body margin. Bases of largest membranelles about 3 µm wide in life. Proximal portion of adoral zone and buccal cavity covered almost entirely by curved buccal lip bearing paroral, which consists of 9–11 widely spaced, about 5 µm long cilia. Buccal cavity flat and narrow, at right bordered by endoral, which is slightly longer than paroral. Pharyngeal fibres clearly recognisable in life and in protargol preparations, extend obliquely backwards.

Cirral pattern and number of cirri rather variable, that is, most variability coefficients >10% (Table 18). Most cirri fine because composed of four cilia only (Fig. 42a, f). Three inconspicuously enlarged frontal cirri arranged in *Gonostomum*-pattern, that is, very near distal end of adoral zone with right and middle cirrus about at same level and left cirrus slightly to distinctly shifted backwards (Fig. 42b, f). In-

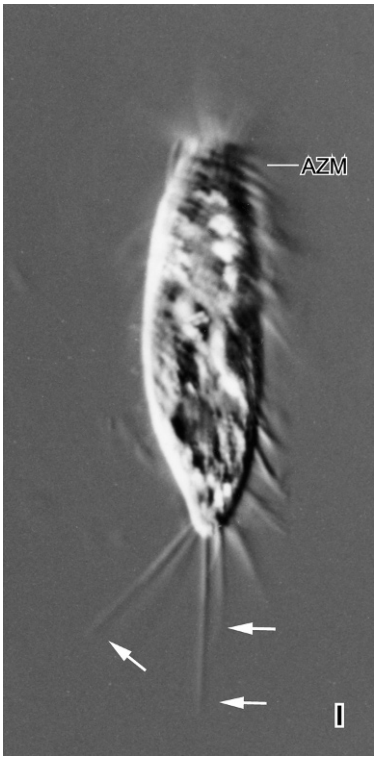


Fig. 42l *Wallackia elegans*, type population (from Foissner et al. 2002a, b. Differential interference contrast micrograph). Ventral view of a freely motile specimen showing, inter alia, the three very long and thus prominent caudal cirri (arrows). AZM = adoral zone of membranelles. Page 227.

variably five (including left frontal cirrus) frontoventral rows: row II (= buccal row) slightly longer than row III, which terminates at 21% of body length on average; row IV slightly shortened anteriorly, terminates at 38% of body length and thus somewhat shorter than adoral zone (46% of body length); row V begins subapically, terminates at 91% of body length and thus on average distinctly longer than right marginal row. Between rear end of frontoventral row V and left marginal row a short row composed of up to five, on average about three cirri, all of them termed transverse cirri in the original description; however, only the rearmost cirrus should, if at all, be designated as transverse cirrus. Because of their position, these "transverse" are difficult to recognise in life. Marginal cirri about 8 µm long in life; right row commences at 10% and terminates at 78% of body length on average; left row begins close to proximal end of adoral zone, ends near rear cell end (Fig. 42a, b, f).

Dorsal bristles about 3 µm long in life, arranged in three kineties (Fig. 42c, g, Table 18). Kinety 1 distinctly shortened, kinety 2 slightly shortened, and kinety 3 almost not shortened anteriorly; kinety 3 often with an increased distance between fourth and fifth kinetid; each kinety associated with a caudal cirrus. Caudal cirri very conspicuous because (i) 33–50% of body length, (ii) thicker than all other cirri, and (iii) Pasteur pipette-shaped; at base about 0.5 µm across; closely spaced at rear cell end, can whip very fast; left and right cirrus each about 20 µm, middle about 25 µm long in life.

Population from Tenerife (Fig. 42i–k, Table 18): Specimens match those from Namibia (= type population) very well, both in general appearance and morphometric details (Table 18). Only the number of "transverse" cirri (see above) is slightly lower (1 or 2 vs. usually 3); thus, this cirral group is hardly distinguishable from marginal and caudal cirri. In addition, very slender specimens (length:width ratio 6:1; Table 18) occur in the Tenerife population.

Cell division: Some dividers of the type population show that only five frontal-ventral cirri anlagen are formed (including the anlage for the undulating membranes and the left frontal cirrus). On average, the three rearmost cirri of anlage IV migrate

posteriorly (Fig. 42h). During interphase, these cirri are arranged between the rear end of the frontoventral row V and the left marginal row. Per definition only the rearmost cirrus of this fragment should be designated as transverse cirrus, if at all because it is not set off from the other cirri.

Occurrence and ecology: Very likely *Wallackia elegans* prefers terrestrial habitats and is possibly confined to the Palaeotropis. Type locality is the Bambatsi Guest Farm (20°10'S 15°25'N; site 49 in Foissner et al. 2002a), Namibia, where we found it in mud and soil from road puddles. Thus, it cannot be excluded that it is a limnetic species. In Namibia, we found it also in the Aubschlucht near the Büllsport Guest Farm in the escarpment of the southern Namib Desert (for detailed description see site 30 in Foissner et al. 2002a). The second population studied by Foissner et al. (2002a, b) is from the light grey, non-saline upper soil layer mixed with few roots and litter (pH 8.2), collected by Brigitte Krassnigg (Salzburg University), from near the beach of Candelaria, Tenerife, Canary Islands. *Wallackia elegans* feeds on bacteria (Foissner et al. 2002a).

Cladotricha Gaievskaïa, 1925

1925 ***Cladotricha* nov. gen.** – Gaievskaïa, Russk. Arkh. Protist., 4: 259 (original description). Type species (by monotypy): *Cladotricha koltzowii* Gaievskaïa, 1925.
1932 ***Cladotricha* Gajevskaja, 1925** – Kahl, Tierwelt Dtl., 25: 540 (revision).
1933 ***Cladotricha* Gajevskaja 1925** – Kahl, Tierwelt N.- u. Ostsee, 23: 105 (guide to marine ciliates).
1938 ***Cladotricha* Gai.** – Ruinen, Zoöl. Meded., Leiden, 20: 249 (brief review and description of five new species).
1950 ***Cladotricha* Gajevskaja** – Kudo, Protozoology, p. 670 (textbook on protozoology).
1961 ***Cladotricha* Gaj.** – Corliss, Ciliated Protozoa, p. 170 (revision of ciliate families).
1977 ***Cladotricha* Gaj.** – Corliss, Trans. Am. microsc. Soc., 96: 137 (classification of ciliate genera).
1979 ***Cladotricha*** – Borror & Evans, J. Protozool., 26: 51 (morphology and cell division of two *Cladotricha* species).
1979 ***Cladotricha* Gajewskaja, 1926** – Corliss, Ciliated Protozoa, p. 309 (revision of ciliates; see nomenclature).
1979 ***Cladotricha* Gajewskaja, 1925** – Jankowski, Trudy zool. Inst., 86: 51 (generic catalogue of hypotrichs; see nomenclature).
1979 ***Cladotricha* Gajewskaja, 1926** – Tuffrau, Trans. Am. microsc. Soc., 98: 525 (revision of hypotrichs; see nomenclature).
1982 ***Cladotricha* Gajewskaja, 1925** [1] – Hemberger, Dissertation, p. 18, 25 (detailed revision of hypotrichs).
1985 ***Cladotricha*** [2] – Small & Lynn, Phylum Ciliophora, p. 456 (guide to ciliate genera; see remarks).
1987 ***Cladotricha* Gajewskaja, 1926** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (revision of hypotrich orders; see nomenclature).

[1] Hemberger (1982) provided the following diagnosis: Je 1 linke und rechte Marginalreihe; 1–3 Ventralreihen; Frontalcirren in 2 Gruppen; 1 Cirrenreihe von 5–8 Cirren, links daneben 2–5 weitere Cirren; keine Transversalcirren; frontal 3 abgetrennte, verlängerte adorale Membranellen; Frontalcirrenentwicklung aus 1–2 longitudinalen Anlagen, Ventralreihenentwicklung aus longitudinalen Anlagen innerhalb der bestehenden Ventralreihen.

[2] Small & Lynn (1985) provided the following characterisation: Frontal cirri not as transverse row of 2–3 at forward end of ventrum.

1992 ***Cladotricha* Gajewskaja, 1926** – Carey, Marine interstitial ciliates, p. 176 (guide to benthic, marine ciliates; see nomenclature).
1994 ***Cladotricha* Gajevskaja, 1925** – Tuffrau & Fleury, Traite de Zoologie, 2: 137 (revision of hypotrich families).
1999 ***Cladotricha* Gajevskaja, 1925** – Shi, Acta Zootax. sinica, 24: 258 (generic revision of hypotrichs).
1999 ***Cladotricha* Gajevskaja, 1925** – Shi, Song & Shi, Progress in Protozoology, p. 106 (generic revision of hypotrichs).
2001 ***Cladotricha* Gajewskaja, 1926** – Aescht, Denisia, 1: 43 (catalogue of generic names of ciliates; see nomenclature).
2001 ***Cladotricha* Gaievskaia, 1925** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 15 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Cladotricha* Gajewskaja, 1926** [1] – Lynn & Small, Phylum Ciliophora, p. 456 (guide to ciliate genera; see nomenclature).
2007 ***Cladotricha* Gajewskaja, 1926** – Jankowski, Phylum Ciliophora, p. 461 (generic revision of ciliates; see nomenclature).
2008 ***Cladotricha* Gajewskaja, 1926** – Lynn, Ciliated protozoa, p. 357 (revision of ciliate families; see nomenclature).
2008 ***Cladotricha* Gaievskaia, 1925** – Berger, Monographiae biol., 88: 467 (brief note on exclusion of genus from the amphisiellids).

Nomenclature: No derivation of the genus-group name is given in the original description or a later paper. *Cladotricha* is a composite of *clado* (from the Greek noun *ho kládos*; the branch) and the Greek noun *he thrix*, *trichos* (the hair); it likely refers to the branched frontal adoral membranelles, which is very probably an artifact (Fig. 43a, b). Feminine gender (Aescht 2001, p. 277). "*Cladotrichia sigmoidea* Ruinen, 1938" in Zimmermann-Timm & Herzig (2006, p. 1945) is an incorrect subsequent spelling of the genus-group name. The name of the author is non-uniformly written (see list of synonyms). The spelling used in the original description (p. 255; N. Gaievskaïa) is used in the present revision.

According to Corliss (1979), Borror & Evans (1979), Aescht (2001), and other workers the original description was published in 1926, a date not supported by other authors (e.g., Kahl 1932, Jankowski 1979, Tuffrau & Fleury 1994). The article about *Cladotricha* was published in issue 3–4 of volume IV of the periodical Archives Russes de Protistologie. Indeed, the latest issue of journals is sometimes published just in the next year. However, I found no hint on the cover or in the table of contents of the journal that this fact applies in the present case. Since there is no problem with synonyms (*Uroleptus packii*, perhaps a synonym of *C. koltzowii* according to Kahl 1932 and Borror 1972, was already described in 1919) I use the date (1925) printed on the journal. *Cladotricha* Gaievskaïa, 1925 is the senior homonym of the trypetid insect *Cladotricha* Hering, 1940 (replaced by *Heringomyia* Hardy, 1968 [not cited in reference section]; details see Evenhuis & Thompson 2004).

Cladotricha Gaievskaïa, 1925 is the name-bearing type genus of the Cladotrichidae[2] Small & Lynn, 1985. Gaievskaïa (1925) established the genus with one species,

[1] Lynn & Small (2002) provided the following characterisation: Body elongate; a portion of the ventral surface barren; one conspicuous ventral cirral file to the left of the right marginal cirral file; transverse cirri, absent.

[2] Small & Lynn (1985, p. 456) provided the following diagnosis: Frontal file, on right, rarely extends past

C. koltzowii. Thus, type fixation is unequivocally by monotypy[1]. The fact that Gaievskaïa (1925) split the species into several subgroups (varieties, forms, morphs; see below) is irrelevant in this respect (ICZN 1999, Article 68.3). According to Aescht (2001), type fixation is by subsequent designation by Jankowski (1979); however, this is obviously incorrect.

Characterisation[2] (A = supposed apomorphy): Gonostomatidae(?) with usually one short and one or two long frontoventral rows. Postoral and pretransverse ventral cirri and transverse cirri lacking (A?). One right and one left marginal row. Three bipolar dorsal kineties, that is, dorsomarginal kineties and kinety fragmentation lacking; each kinety with a caudal cirrus. Long frontoventral rows originate by intrakinetal proliferation. Highly saline habitats (A?).

Additional characters: Since most species presently assigned to *Cladotricha* are not described in every detail, the present list is rather uncertain and incomplete. Body usually elongate, flexible, but not distinctly contractile. Body shape and cirral pattern rather variable, likely because of extreme habitat. Contractile vacuole lacking or rarely and slowly contracting, usually somewhat displaced inwards. Two, four, or many macronuclear nodules; type species according to original description, however, with only one macronuclear nodule (misobservation?). Cortical granules likely lacking. Cytoplasm strongly vacuolised. Dorsal bristles short, that is, usually 2–4 µm. Resting cysts present.

Remarks: See nomenclature before reading the remarks! The systematics of *Cladotricha* is a difficult task, including the higher level classification. So far, *Cladotricha* has been assigned to nine(!) different higher taxa, demonstrating the great uncertainty, which is mainly due to the rather incomplete characterisation of the type species.

Gaievskaïa (1925) classified *Cladotricha* in the subfamily Urostylinae Bütschli, 1889. In Kahl (1932), who classified all non-euplotid hypotrichs in the oxytrichids, *Cladotricha* is the first genus of the hypotrichs indicating that he considered it as rather basal group. On page 541 he discussed that *C. koltzowii*, type and sole species known at that time, is perhaps closely related or even identical with *Uroleptus packii* Calkins in Pack (1919), which Kahl (1932, p. 554) has transferred to *Strongylidium*. Ruinen (1938) provided a rather detailed characterisation of the genus (see below),

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mid-body; at least 1 left and 1 right marginal files.

[1] According to the ICZN (1999, Article 68.2.1) the expression "gen. n., sp. n.", or an equivalent, applied before 1931 to only one of two or more new nominal species originally included in a new nominal genus, are deemed to be an original designation if no other type was explicitly designated. Since the original description of *Cladotricha* contains only one species (*C. koltzowii*) this article does actually not apply. Thus, strictly speaking type fixation was by monotypy (Article 68.3). When the various subgroups of *C. koltzowii* described by Gaievskaïa (1925) are raised to species rank, then the form "*Cladotricha koltzowii typika*" (p. 259) becomes the type of *C. koltzowii* (however, under the name *C. koltzowii*, and not as *Cladotricha typika* [this name is disclaimed for nomenclatural purposes; ICZN 1999, Article 8.3]) although the procedure explained in Article 68.2.2 of the ICZN (1999) is not explicitly applicable to taxa below the species-level.

[2] The characterisation of *Cladotricha* is rather vague and in great need of improvement because the type species is insufficiently characterised and the congenerity of the other species included not quite certain.

but made no comment about the classification. Kudo (1950) and Corliss (1961) obviously followed Kahl and assigned *Cladotricha* to the Oxytrichidae.

Borror (1972, p. 13) eventually synonymised *C. koltzowii* with *U. packii*, and simultaneously classified – obviously again following Kahl (1932) – *Uroleptus packii* in *Strongylidium* Sterki, 1878. He assigned *Strongylidium* to the spirofilids, together with *Hypotrichidium*, *Atractos*, *Chaetospira*, *Spiratella*, *Stichotricha*, and *Urostrongylum*. Thus, Borror (1972) synonymised *Cladotricha* with *Strongylidium*, an act not discussed by Paiva & Silva-Neto (2007) in their brief revision about *Strongylidium* (for comparison of *Cladotricha* and *Strongylidium*, see below).

Corliss (1977) neither affirmed the synonymy proposed by Borror nor did he classify it in the spirofilids. He assigned *Cladotricha* to the strongyliidids, together with *Chaetospira*, *Klonostricha*, *Strongylidium*, and *Urostrongylum*, obviously because of the sometimes more or less distinctly twisted body. In his opus magnum, Corliss was uncertain about this higher level classification and therefore mentioned it as incertae sedis in the Strongylidiidae Fauré-Fremiet, 1961a (Corliss 1979). Simultaneously, Borror & Evans (1979) reactivated *Cladotricha* and suggested a separation of the "series" *Kahliella-Cladotricha-Uroleptoides* from the tubicolous and planktonic spirofilids. Tuffrau (1979, 1987) and Tuffrau & Fleury (1994) assigned it to the Kahliellidae, a proposal followed by Lynn & Small (2002), Jankowski (2007), and Lynn (2008). I abandon the classification in the kahliellids because the sparse data about the type species indicate that no parental ciliature is retained in the postdivider, a main feature of the kahliellids. The dorsal kinety pattern of the type species *C. koltzowii* is not known, but that of the well described species is obviously identical with that of the last common ancestor of the hypotrichs and which was obviously taken over by the gonostomatids, namely three bipolar kineties each bearing a caudal cirrus, that is, a dorsomarginal row – present in *Kahliella* – is lacking in *Cladotricha*.

Hemberger (1982) classified *Cladotricha* in the Amphisiellidae. However, in this group the median cirral row is formed from two or three anlagen, whereas in *Cladotricha* such mixed rows (Berger 2008, p. 2) are lacking. Thus, the classification proposed by Hemberger is likely incorrect. According to Curds et al. (1983, p. 420), *Cladotricha* is – like *Platytrichotus* Stokes, 1886 – a junior synonym of *Uroleptus* Ehrenberg, 1831. But a synonymy of *Cladotricha* and *Uroleptus* is very unlikely, because the two ventral cirral rows of *Cladotricha* do not form a zigzagging midventral pattern which is so characteristic for *Uroleptus*, and its synonym *Platytrichotus* (Kahl 1932, p. 550; Borror 1972, p. 12).

Small & Lynn (1985, p. 456) established the family Cladotrichidae with *Cladotricha* as name-bearing type genus. Aside from that, the group contained *Engelmanniella* (p. 498), *Uroleptoides* (for review, see Berger 2008, p. 224), *Lamtostyla* (for review, see Berger 2008, p. 161), and *Perisincirra* (p. 463). Later, Lynn followed Tuffrau (1979) and submerged *Cladotricha* and the cladotrichids in the kahliellids (Lynn & Small 2002, Lynn 2008). In the present review *Cladotricha* is classified in

the gonostomatids, that is, the cladotrichids are synonymised with the Gonostomatidae.

Eigner (1999, p. 46) assigned *Cladotricha koltzowii* to the Orthoamphisiellidae because in the rightmost frontoventral row an anlage is formed. However, *Orthoamphisiella stramenticola*, type of the genus, does not have a gonostomatid oral apparatus (Eigner & Foissner 1991, 1993); unfortunately, *O. stramenticola* is not yet gene-sequenced so that the phylogenetic position of *Orthoamphisiella* based on molecular data is not yet known. By contrast, *Orthoamphisiella breviseries*, a species from a highly saline soil from the margin of the Etosha Pan (Namibia) has a gonostomatid adoral zone, and the 18S rDNA gene sequence data in some trees indicate a close relationship with some *Gonostomum* species (e.g., Foissner et al. 2002a, 2004, Shao et al. 2007); other trees, however, do not support a close affinity of *O. breviseries* and *Gonostomum* (Gong et al. 2007, Foissner & Stoeck 2008, Shao et al. 2008, Sonntag et al. 2008, Paiva et al. 2009). Thus, the relationship of *Orthoamphisiella* and *Gonostomum* remains uncertain.

Shi (1999) and Shi et al. (1999) classified *Cladotricha* in the Keronopsidae, together with *Keronopsis*, *Parakeronopsis*, *Erniella*, *Pseudouroleptus* (for review, see Berger 2008, p. 658), *Pelagotrichidium*, *Wallackia* (p. 206), *Paraurostyla* (for review, see Berger 1999, p. 841), and *Gonostomum* (p. 58). However, the keronopsids as defined by the Chinese workers seem to be a rather inhomogeneous assemblage, inter alia, because *Keronopsis* and its sistergroup *Paraholosticha* are the sole hypotrichs which divide in cysts; in addition, there are significant differences in the dorsal kinety pattern and its morphogenesis between the genera included.

As mentioned above, the original description of the type species is not very detailed and the available redescriptions lack some main features (e.g., exact cirral pattern and dorsal infraciliature including its morphogenesis) making a serious classification basically impossible. Thus, I preliminary assign *Cladotricha* to the Gonostomatidae because the adoral zone of the type species is reminiscent of that of *Gonostomum* (Gaievskaïa 1925, Ruinen 1938, Borror & Evans 1979). In addition, the undulating membrane pattern and, less important because plesiomorphic, the dorsal kinety pattern of the well-studied species (e.g., *Cladotricha australis*) are as in *Gonostomum*. For a foundation of the exclusion of *Cladotricha* from the kahliellids see above. Further studies will show whether *Cladotricha* is a monophyletic group or just an amassing of species preferring highly saline habitats (Berger 2008, p. 517). Perhaps *Cladotricha* is the halophilous sister group of *Gonostomum* and/or *Wallackia*. All species, except *C. australis* and *C. halophila*, have to be neotypified.

Ruinen (1938) redescribed *C. koltzowii* and discovered five new *Cladotricha* species from saturated saltwater habitats from Portugal, the Indian subcontinent, and South-Australia. The samples studied by Ruinen have been collected by L. G. M. Baas Becking and investigated under the technical supervision of Alfred Kahl (Hamburg), that is, the descriptions have a rather high quality, although based on live observations only. The samples are from highly concentrated brines, raw salt, or saline sludge and have been studied directly or after cultivation in tap water or Van Niel-

scher nutritive solution. I preliminary accept all species described by Ruinen (1938) because it is too early to make a final decision about the synonymy of certain populations; however, three of them (*C. elongata*, *C. kahli*, *C. variabilis*) are removed from *Cladotricha* because they lack a long frontoventral row and have postoral ventral cirri. They are classified as incertae sedis in *Apourosomoida* (p. 684). All species have to be redescribed in great detail because important features are lacking or only insufficiently known. Ruinen (1938) provided a detailed characterisation of the genus which is given here (as translation) because it contains meaningful data not repeated in the individual species descriptions: Ciliates from hypersaline waters. Body outline elongate to slender, fusiform, round in cross-section to ribbon-shaped, sometimes widened in the anterior or middle portion, rear end rounded or cuspidate. Body very flexible, not contractile. Oral apparatus mainly lateral, with strong adoral zone. Buccal lip high, covering buccal cavity. Undulating membrane (likely Ruinen meant the paroral) rudimentary or weakly developed (which agrees with *Gonostomum*). Two or three frontal (distal) membranelles which serve to swim; according to Gaievskaïa (1925) these membranelles are tattered, a feature of moribund specimens according to Ruinen (1938). Two marginal rows, the right one commences with 4–6 cirri on the dorsal side. Ventral rows usually as single row or rudimentary. Dorsal kineties lacking, in some species rudimentary. Transverse cirri lacking. On frontal area some isolated cirri, but not always in the same number and pattern; usually three cirri anteriorly and 2–4 behind. Cytoplasm highly vacuolised. Nuclear apparatus composed of two long or globular macronuclear nodules with small, globular micronuclei attached. Food composed of green and colourless flagellates, cyanobacteria, small diatoms, and bacteria.

As mentioned above, Borror (1972) submerged *Cladotricha* in *Strongylidium* in that he synonymised the type species *C. koltzowii* Gaievskaïa, 1925 with *Strongylidium packii* (Calkins in Pack, 1919) Kahl, 1932. Type species of *Strongylidium* is the limnetic *S. crassum* Sterki, 1878, illustrated for the first time by Kahl (1932, p. 551)[1]. Admittedly, a separation of these two genera is difficult because both type species are not described in detail, that is, important features, e.g., oral apparatus, exact cirral pattern, and dorsal infraciliature are not known. Thus, a final decision can only be made when both species are characterised with modern methods. At present, *Cladotricha* and *Strongylidium* can be separated via the two insufficiently described type species only rather vague by the habitat (highly saline habitats vs. limnetic, other species are terrestrial or marine; note that the monophyly of *Strongylidium* is as questionable as that of *Cladotricha*), the adoral zone (roughly gonostomatid vs. ordinary), and the torsion of the cirral pattern (lacking to inconspicuous vs. distinct). When well-investigated species like, for example, *Cladotricha australis* (Blatterer & Foissner 1988) and *Strongylidium pseudocrassum* (Paiva & Silva-Neto 2007) are included in the comparison, then the separation by the oral apparatus (gonostomatid vs. ordinary) is unambiguous and a synonymy is beyond debate.

[1] The redescription by Lokot (1987, p. 72) is less detailed than that by Kahl (1932).

Pomp & Wilbert (1988, p. 482) found an unidentified *Cladotricha* species in alkaline soil near Adelaide, Southern Australia.

For separation of *Cladotricha* from other genera of the Gonostomatidae, see chapter "Genera included in the Gonostomatidae" and key on p. 57. For separation from *Apourosomoida*, see p. 684.

Species included in *Cladotricha* (alphabetically arranged basionyms or provisional names are given): (1) *Cladotricha australis* Blatterer & Foissner, 1988; (2) *Cladotricha koltzowii* Gaievskaïa, 1925 (type); (3) *Cladotricha* nov. spec. in Nießen (1984); (4) *Cladotricha sagittata* Ruinen, 1938; (5) *Cladotricha sigmoidea* Ruinen, 1938; (6) *Cladotricha* spec. in Nießen (1984). Incertae sedis: (7) *Uroleptus packii* Calkins in Pack, 1919.

Species misclassified in *Cladotricha*: The following species – originally classified in *Cladotricha* – have been transferred to *Apourosomoida* because their cirral pattern differs too distinctly from that of the other ("true") *Cladotricha* species.

Cladotricha elongata Ruinen, 1938. Remarks: Now *Apourosomoida elongata* (p. 687).

Cladotricha kahli Ruinen, 1938. Remarks: Now *Apourosomoida kahli* (p. 689).

Cladotricha variabilis Ruinen, 1938. Remarks: Now *Apourosomoida variabilis* (p. 690).

Key to *Cladotricha* species

Identification of *Cladotricha* species is a difficult task especially because most species are not yet described in detail. In addition, the variability is rather high, likely due to the high salinity of the habitats. Because of these uncertainties, the key is not very accurate and the type species occurs at several sites of the key. If you go round in circles with the key below check the illustrations and descriptions. The key also contains three *Cladotricha* species now classified in *Apourosomoida* because postoral ventral cirri are present and a long frontoventral row is lacking. *Wallackia bujoreani* and some other gonostomatids sometimes also occur in saline soil (p. 212).

1 Macronucleus composed of more than four (5–28) nodules (Fig. 48a, 49a). **2**
- Macronucleus composed of 1, 2, or 4 nodules (e.g., Fig. 43a, j–l). **3**

2 One buccal cirrus; 5–14, on average 9.6 macronuclear nodules (Fig. 49a–d). . . . . *Cladotricha halophila* (p. 270)
- 1–5, on average 3.3 buccal cirri; 13–28, on average 18.4 macronuclear nodules (Fig. 48a–l). . . . . *Cladotricha australis* (p. 262)

3 (1) One macronucleus (Fig. 43a–h). . . . . *Cladotricha koltzowii* (p. 242)
- Two or four macronuclear nodules. **4**

4 Four macronuclear nodules (e.g., Fig. 43k, l, m, 113a, 114a). **5**
- Two macronuclear nodules (e.g., Fig. 43j, 44a, 45a–c, 47a, 50a, 112a). **7**

5 Two pairs of macronuclear nodules with each one micronucleus in between; frontoventral row long; two prominent distal adoral membranelles; postoral cirri lacking (Fig. 43k, m). . . . . *Cladotricha koltzowii* (p. 242)
- Nuclear apparatus not as above; long frontoventral lacking; three prominent distal adoral membranelles; postoral cirri present (Fig. 113a, 114a). **6**

6 Two postoral ventral cirri (Fig. 113a). . . . . *Apourosomoida kahli* (p. 689)
- About 6 postoral ventral cirri (Fig. 114a, h). . *Apourosomoida variabilis* (p. 690)

7 (4) Two long frontoventral rows (Fig. 43j, 44a). **8**
- None or one long frontoventral row (Fig. 45a, 46a, 47a, 50a, 112a). **9**

8 Posterior body end tailed, without(?) prominent cirri (Fig. 43j). . . . . *Cladotricha koltzowii* (p. 242)
- Posterior body end rounded, with three prominent cirri (Fig. 44a). . . . . *Cladotricha sagittata* (p. 252)

9 (7) One micronucleus in between macronuclear nodules (Fig. 112a). . . . . *Apourosomoida elongata* (p. 687)
- Nuclear apparatus not as above. **10**

10 Body sigmoidal (Fig. 45a, 50a). **12**
- Body not sigmoidal **11**

11 Cirral row between rear portion of marginal rows present (Fig. 47a, c). . . . . *Cladotricha* spec. in Nießen (1984) (p. 260)
- Cirral row between rear portion of marginal rows lacking (Fig. 46a). . . . . *Cladotricha* spec. in Nießen (1984) (p. 256)

12 (10) Body pale green likely due to symbiotic algae (Fig. 50a, b). . . . . *Strongylidium packii* (p. 276)
- Body not green (Fig. 45a). . . . . *Cladotricha sigmoidea* (p. 254)

Cladotricha koltzowii Gaievskaïa, 1925
(Fig. 43a–s)

1924 ***Cladotricha koltzowii* Gayew.** – Gayewskaya, Russki gidrobiol. Zh., 3: 244, 251 (nomen nudum because not accompanied by morphological description).

1925 ***Cladotricha koltzowii* nov. gen. nov. sp.** – Gaievskaïa, Russk. Arkh. Protist., 4: 255, 281, Planche XV, fig. 1–9 (Fig. 43a–i; original description; very likely no type material available).

1925 ***Cladotricha koltzowii* nov. gen. hov. sp. forma *typika*** – Gaievskaïa, Russk. Arkh. Protist., 4: 259, Planche XV, fig. 1, 2, 8, 9 (Fig. 43a, b, h, i; original description of nominotypical form).

1925 ***Cladotricha koltzowii* morpha *minima*** – Gaievskaïa, Russk. Arkh. Protist., 4: 273, Planche XV, fig. 3 (Fig. 43c; original description of morph).

1925 ***Cladotricha koltzowii* var. *spiralis*** – Gaievskaïa, Russk. Arkh. Protist., 4: 275, 278, Planche XV, fig. 5 (Fig. 43e; original description of variety).

1925 ***Cladotricha koltzowii* var.? morpha? *pisciformis*** – Gaievskaïa, Russk. Arkh. Protist., 4: 275, 278, Planche XV, fig. 6 (Fig. 43f; original description of variety or morph).

1925 ***Cladotricha koltzowii* var. *gigas*** – Gaievskaïa, Russk. Arkh. Protist., 4: 277, Planche XV, fig. 7 (Fig. 43g; original description of variety).

1925 ***Cladotricha koltzowii* var. *lata*** – Gaievskaïa, Russk. Arkh. Protist., 4: 274, 278, Planche XV, fig. 4 (Fig. 43d; original description).

1932 ***Cladotricha koltzowii* Gaj., 1925** – Kahl, Tierwelt Dtl., 25: 540, Fig. 86$_{4, 5}$ (Fig. 43l1, l2; detailed revision).
1933 ***Cladotricha koltzowii* Gajevskaja 1925** – Kahl, Tierwelt N.- u. Ostsee, 23: 105, Fig. 16.1 (Fig. 43l3, l4; guide to marine ciliates).
1937 ***Cladotricha koltzowii*** – Gelei, Arch. Protistenk., 88: 319, Abb. 5b (redrawing of Fig. 43g; review about spiralled ciliates).
1938 ***Cladotricha koltzowii* Gai.** – Ruinen, Zoöl. Meded., Leiden, 20: 250, Fig. 5a–c (Fig. 43j–l; redescription; very likely no voucher material available).
1950 ***Cladotricha koltzowii* G.** – Kudo, Protozoology, p. 670, Fig. 314k, l (Fig. 43l1, l2; textbook on protozoology).
1979 ***Cladotricha koltzowii* Gajewskaja, 1926** – Borror & Evans, J. Protozool., 26: 52, Fig. 6–12 (Fig. 43m–s; description of a Great Salt Lake population and cell division; site not mentioned were vouchers slides deposited; see nomenclature).
1982 ***Cladotricha koltzowii* Gajewskaja, 1925** – Hemberger, Dissertation, p. 25 (detailed revision of hypotrichs).
1985 ***Cladotricha koltzowi*** – Small & Lynn, Phylum Ciliophora, p. 456, Fig. 25 (Fig. 43m; guide to ciliate genera; incorrect subsequent spelling).
1992 ***Cladotricha koltzowii* Gajewskaja, 1926** – Carey, Marine interstitial ciliates, p. 176 (Fig. 694; redrawing of Fig. 43a [see remarks]; guide to benthic, marine ciliates; see nomenclature).
2001 ***Cladotricha koltzowii* Gaievskaia, 1925** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 15 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Cladotricha kolzowi*** – Lynn & Small, Phylum Ciliophora, p. 456, Fig. 50 (Fig. 43m; guide to ciliate genera; incorrect subsequent spelling).
2007 ***Cladotricha koltzowi*** – Jankowski, Phylum Ciliophora, p. 461 (generic revision of ciliates; incorrect subsequent spelling).

Nomenclature: I found no derivation of the species-group name in the original description. Obviously Gaievskaïa (1925) dedicated this species to a person with the surname Koltzow; perhaps this is a different spelling of N. K. Kolcov or N. K. Koltzoff, who wrote some papers about peritrichs (e.g., Dogiel 1965, p. 691). Type species of *Cladotricha* Gaievskaïa, 1925. The forma name *typik·us*, *-a*, *-um* (Greek adjective [m; f; n]; typical, archetypal, normal, authentic) indicates that this form is the "normal" or "typical" form[1] (Fig. 43a, b, h, i). The morpha name *minim·us*, *-a*, *-um* (superlative of *parvus*; smallest, least, very small) alludes to the small size of this specimen(s) (Fig. 43c). The variety name *spiral·is*, *-is*, *-e* (Greek adjective [m; f; n]; serpentine, spiral, twisted) alludes to the twisted body (Fig. 43e). The variety or morpha name *pisciform·is*, *-is*, *-e* is a composite of the Latin noun *piscis* (fish) and the Latin *formis* (a species looking like another species/taxon) and was obviously used because the specimen has roughly the shape of a fish (Fig. 43f). The variety name *gigas* (Greek; huge, colossal, gigantic) obviously alludes to the large size of the corresponding specimen(s) (Fig. 43g). The variety name *lat·us*, *-a*, *-um* (Latin adjective [m; f; n]; wide, broad, expanded) obviously alludes to the wide body of the corresponding specimen(s) (Fig. 43d). For discussion of the year of publication (1925 or 1926), see genus section.

[1] Note that the name of the nominotypical variety, form, or morph is always *Cladotricha koltzowii koltzowii* Gaievskaïa 1925 (autonym; Winston 1999, p. 330), that is, the forma name *typikus* is actually superfluous.

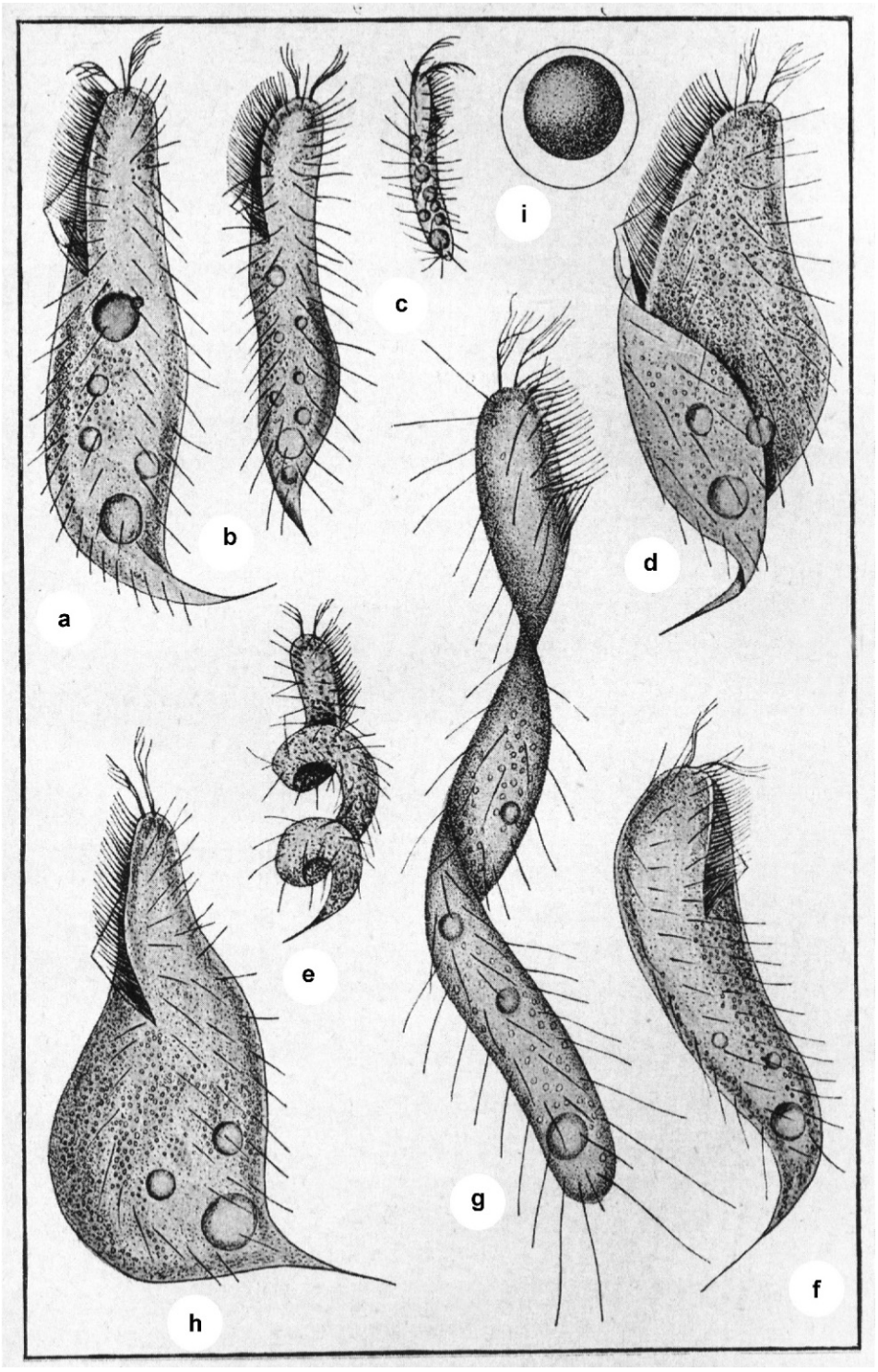
Incorrect subsequent spellings (see also list of synonyms): *Cladotricha coltzowi* Gaew. (Dagajeva 1930, p. 35); *Cladotricha kolzowii* (Borror 1972, p. 13; Borror & Wicklow 1982); *Cladotricha koltzowi* (Jankowski 1979, p. 51; Agamaliev 1983, p. 36; 1990, p. 61; Fernandez-Leborans & Novillo 1993, p. 216; 1994a, p. 27; Aescht 2001, p. 43, 277); *Cladotricha koltzowwi* (Petran 1977, p. 97); *Cladotricha kotzlowii* (Shi et al. 1999, p. 106; Lei et al. 2009, p. 310). *Strongylidium koltzowii* in Agamaliev (1980, p. 336) is a combination which was obviously never made formally. When further studies show that *Cladotricha* is indeed the junior synonym of *Strongylidium*, then *C. koltzowii* has to be combined formally.

Remarks: For the numerous higher level classifications of *Cladotricha*, respectively, its type species *C. koltzowii*, see genus section.

Gaievskaïa (1925) discovered this species in a highly saline habitat from the Black Sea peninsula Crimea. It is generally known that species from such extreme habitats (salt concentration up to 230‰!) are rather variable in many features. The high variability mainly in body shape and size caused Gaievskaïa (1925) to establish six varieties, forms, and morphs (Fig. 43a–h). The French original description is rather long. I did not translate the paper in every detail, but extracted the main features available from the text and the illustrations. The description is, according to the state-of-the-art, based on life observations and various staining methods only so that details (e.g., exact cirral pattern, oral ciliature, dorsal kinety pattern) of the infraciliature remain unknown making a detailed characterisation of *Cladotricha* and a comparison with other species very difficult. The nuclear apparatus was stained with Delafield's hematoxylin. Thus, it is somewhat surprising that this species shall have only one macronuclear nodule, a rather uncommon, but not impossible feature for a hypotrich. Whether this is the ordinary pattern, a postconjugant (conjugation was observed), or a misobservation (second nodule overlooked; see note on review by Carey 1992 below) is not known. By contrast, Ruinen (1938) and Borror & Evans (1979) described only specimens with two or four nodules. This significant difference in the descriptions and the unknown dorsal kinety pattern are the major reasons necessitating a neotypification of the type species. As requested by the ICZN (1999), the neotype has to come from or very near the original type locality to minimise the possibility of a misidentification.

Ruinen (1938) found *Cladotricha koltzowii* at three sites. Unfortunately, he did not indicate which population/illustration (Fig. 43j–l) refers to which site. Borror & Evans (1979) did not provided live data and morphometrics.

Fig. 43a–i *Cladotricha koltzowii* (from Gaievskaïa 1925. From life and after staining. Drawn to scale. In a, b, d, h, the ventral infraciliature is shown as seen from the dorsal side). **a, b, h:** Variability of *Cladotricha koltzowii* forma *typika*, a = 94 × 24 µm (50‰ salt content), b = 78 × 16 µm (170‰), h = 88 × 44 µm (70‰). Note the single macronucleus close to the buccal vertex with attached micronucleus (a; a misobservation?). **c:** *Cladotricha koltzowii* morpha *minima*, 35 × 5 µm (230‰). **d:** *Cladotricha koltzowii* variety *lata*, 116 × 72 µm (60‰). **e:** *Cladotricha koltzowii* variety *spiralis*, 80 × 6 µm (60‰). **f:** *Cladotricha koltzowii* variety? morpha? *pisciformis*, 88 × 22 µm (60‰). **g:** *Cladotricha koltzowii* variety *gigas*, 168 × 18 µm (70‰). **i:** Resting cyst of *Cladotricha koltzowii* forma *typika*, 24 µm. Page 242. →


a
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Uroleptus packii Calkins in Pack, 1919 – a little known species transferred to *Strongylidium* by Kahl (1932) – is perhaps a synonym of *C. koltzowii* according to Kahl (1932) and Borror (1972, p. 13; see also genus section). As many other species, *Uroleptus packii* was not described in detail preventing a serious final classification (Fig. 50a–e). The main difference between the two original descriptions (Pack 1919, Gaievskaïa 1925) is, aside from the number of macronuclear nodules (two vs. one [uncertain]), in the number of long frontoventral rows, namely one in *U. packii* against two in *C. koltzowii*. In my mind, *Uroleptus packii* resembles *C. sigmoidea* as concerns the twisted body and the arrangement of the cirri. The main difference is in the symbiotic algae, which are very likely present in *U. packii*, but lacking in *C. sigmoidea*. Thus, I preliminary classify *U. packii* as incertae sedis in *Cladotricha*, especially because it was discovered, like the *C. koltzowii*-population described by Borror & Evans (1979), in the highly saline Great Salt Lake in Utah, USA.

According to Hemberger (1982), *Cladotricha sagittata* (Fig. 44a) and *C. sigmoidea* (Fig. 45a–f) are junior synonyms of *C. koltzowii*. Indeed, the cirral pattern (one long frontoventral row) of these two species is similar to that of the Great Salt Lake *C. koltzowii* population described by Borror & Evans (1979, Fig. 43m) and one population described by Ruinen (1938, Fig. 43k). However, the type population of *C. koltzowii* has two long frontoventral rows (Fig. 43a–h) so that the proposed synonymy is not certain. Thus, I suggest to keep the species separate until more detailed data about this group are available.

Carey (1992) made a redrawing of Fig. 43a and obviously interpreted the large globule in the posterior portion of the cell as second macronuclear nodule, which would correspond very well one description by Ruinen (1938, Fig. 43j). However, material from the type locality (Lake Solenoïé near Sevastopol) has to be studied to get a final decision about the nuclear apparatus. When only binucleate specimens occur it is safe to assume that the single macronucleus described by Gaievskaïa (1925) is a misobservation.

The description of the limnetic population investigated by Madrazo-Garibay & López-Ochoterena (1973) is insufficient (Fig. 51a).

Morphology: As discussed above, the original description contains some uncertainties and the redescriptions by Ruinen (1938) and Borror & Evans (1979) differ from the original description in some important features. Thus, I do not provide a combined description, but keep the populations separate because it cannot be excluded that two or more species are mixed up.

Type population described by Gaievskaïa (1925; Fig. 43a–h): At first the nominotypical form ("*typika*") is characterised (Fig. 43a, b, h), followed by a brief listing of the deviating features of the aberrant specimens (Fig. 43c–g). Body size of nominotypical form at 50‰ salinity about 92–96 × 24 µm, that is, length:width ratio about 4:1. Body outline roughly elongate fusiform, anterior end rounded; posterior portion tapered like a thorn, usually(?) curved onto right side (Fig. 43a, b); however, wide ("monstrous" according to Gaievskaïa 1925) specimens also present (Fig. 43h). Ventral side flat, dorsal side convex. Body flexible, not contractile; not distinctly

twisted according to illustrations. Only one spherical macronuclear nodule slightly behind level of buccal vertex with one small globular micronucleus attached (see remarks). Contractile vacuole lacking (see also Gayewskaya 1924, p. 251). Presence/absence of cortical granules not mentioned. Cytoplasm with several non-contractile vacuoles (termed "vacuolae aquilegiae" by Gaievskaïa 1925, p. 267); their number increases with increasing salt content of medium. Movement mainly accomplished by the anteriormost, fringed adoral membranelles. The following description of the oral apparatus and cirral pattern is mainly based on the illustrations. Adoral zone occupies about one third of body length in specimen shown in Fig. 43a; anteriormost membranelles ramified (artifact?) and mainly responsible for movement; main portion extends, as in *Gonostomum*, along anterior left body margin, proximal portion, however, not distinctly curved inwards. Distal end of adoral zone obviously not extending posteriorly. Buccal cavity obviously very small, undulating membrane (likely paroral) forms triangular sail (Fig. 43a, b, h). Cytopharynx lacking (misobservation?). No distinctly enlarged frontal cirri recognisable. Invariable four cirral rows, namely two long, clearly separated frontoventral rows indicating that no midventral pattern is present; extend about to base of narrowed posterior body portion. Transverse cirri obviously lacking. Left marginal row commences close to buccal vertex, extends to near cell end, composed of about 17 cirri in specimen illustrated (Fig. 43a; value must not be overinterpreted); right marginal row begins likely near distal end of adoral zone. Dorsal bristles lacking (probably this is a misobservation although one cannot exclude that this part of the infraciliature has been lost).

Cladotricha koltzowii morpha *minima* (Fig. 43c): Body size 35 × 5 µm, likely mainly occurring at high salt content (230‰). Body slender, elongate, rear end not distinctly tailed. Cytoplasm strongly vacuolised.

Cladotricha koltzowii variety *lata* (Fig. 43d): Body size 116 × 72 µm, that is body very wide fusiform; anterior end rounded, posterior portion tapered, and twisted in specimen illustrated.

Cladotricha koltzowii variety *spiralis* (Fig. 43e): Body size 80 × 6 µm, that is, very slender (length:width ratio about 13:1); strongly twisted like a spirillum.

Cladotricha koltzowii morpha? variety? *pisciformis* (Fig. 43f): Body 88 × 22 µm, that is, length:width ratio 4:1 as in typical form, but body widest in anterior portion and continuously tapering posteriorly ending with fine tail.

Cladotricha koltzowii variety *gigas* (Fig. 43g): Body size 168 × 18 µm, that is, length:width ratio 9.3:1. Body vermiform, heavily twisted about main body axis; like variety *spiralis*, but not so strongly squeezed together.

Population(s) studied by Ruinen (1938): Body length 100–160 µm; length:width ratio 3.5–7.0:1, specimen shown in Fig. 43k about 6:1, that is, body slender, band-shaped; rear cell end cuspidate, turned rightwards in both specimens illustrated; body shape, including spine at end, slightly variable. Body often twisted about main body axis. Nuclear apparatus according to Ruinen (1938) typically composed of two stretched macronuclear nodules (20 × 6 µm) with attached, globular micronuclei about 3 µm across; according to Fig. 43j–l, however, nuclear apparatus rather vari-

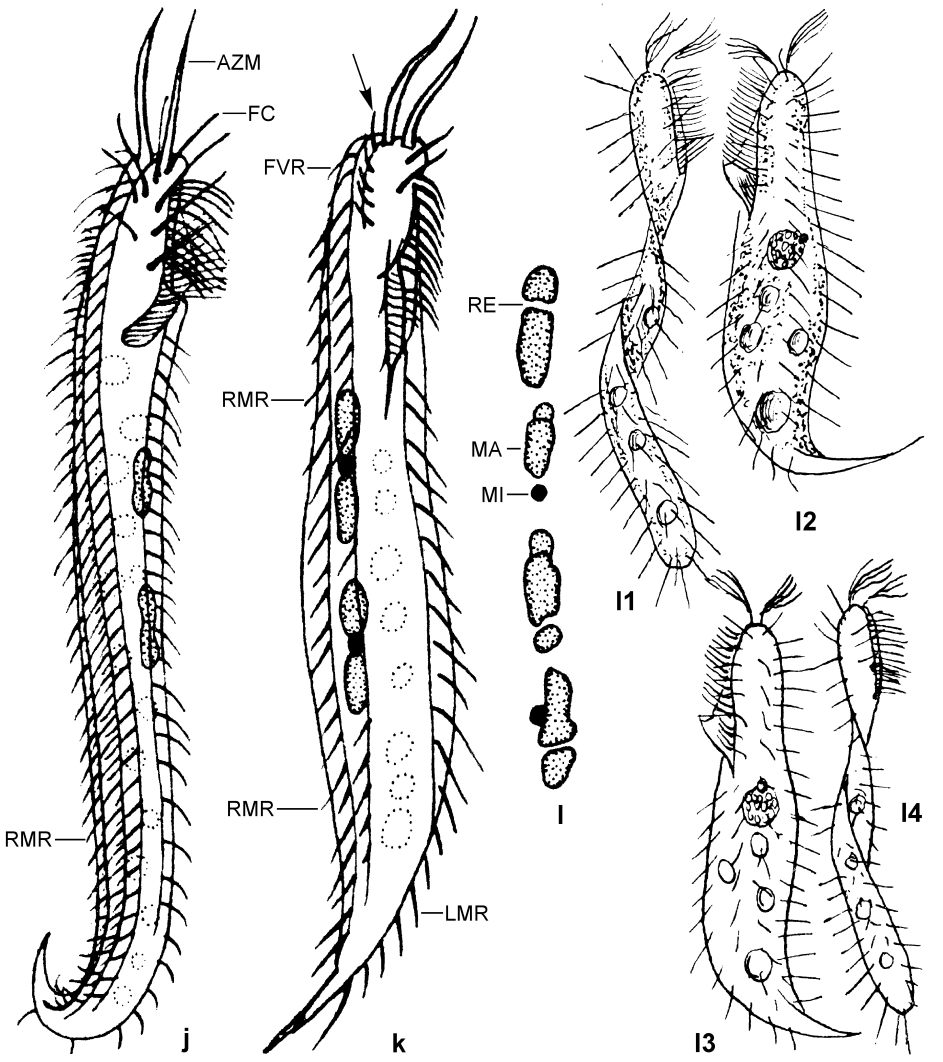


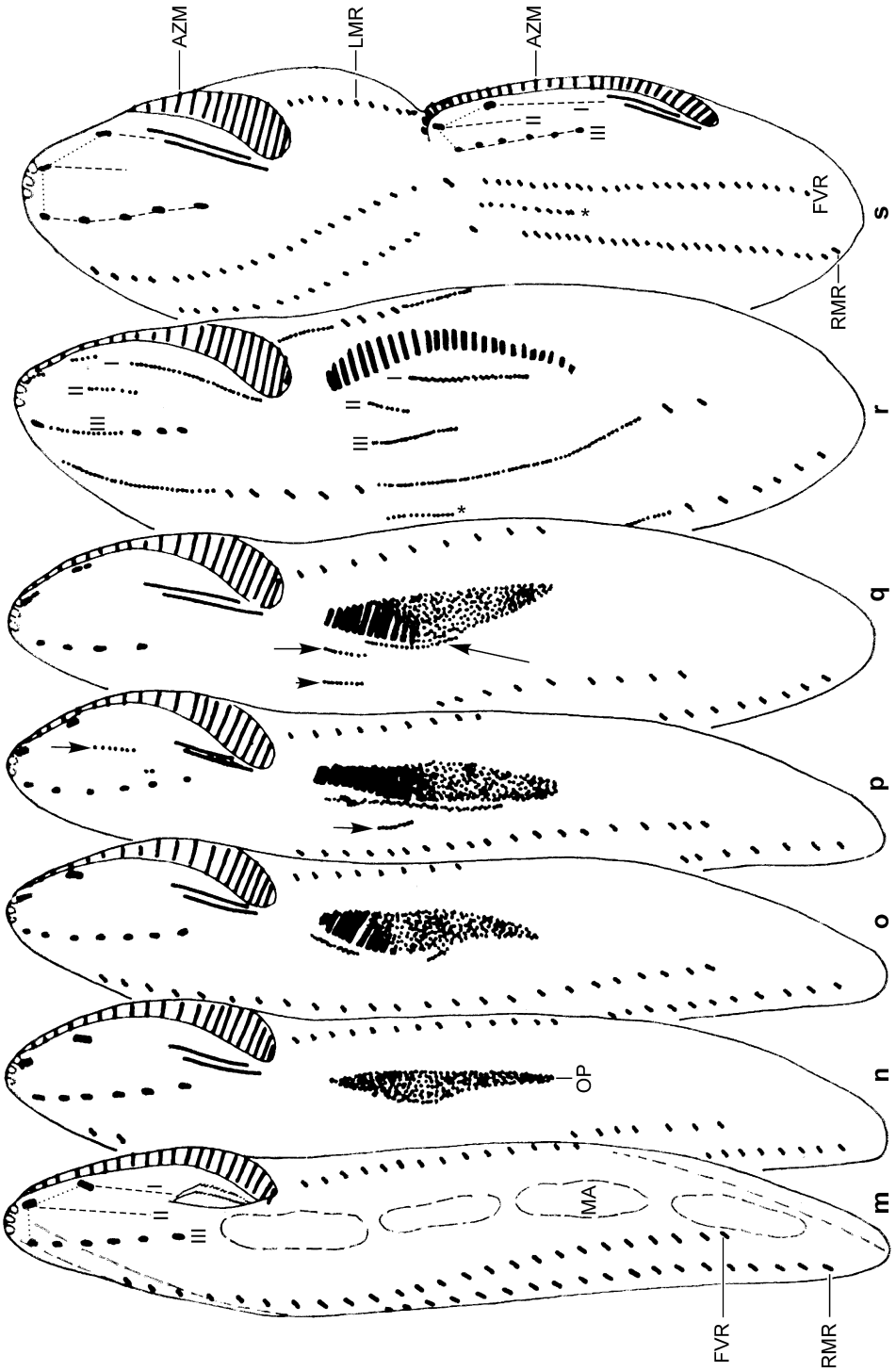
Fig. 43j–l4 *Cladotricha koltzowii* (j–l, from Ruinen 1938; l1, l2, after Gaievskaïa 1925 from Kahl 1932; l3, l4, after Gaievskaïa 1925 from Kahl 1933. From life). **j:** Ventral view of specimen with two long frontoventral rows and two macronuclear nodules, individual size not indicated. **k:** Ventral view of specimen with one long frontoventral row and four macronuclear nodules arranged in two pairs with each one micronucleus in between. Arrow marks anteriormost cirrus of short frontoventral row. Note that this specimen closely resembles the population studied by Borror & Evans (1979; Fig. 43m). **l:** Nuclear apparatus. Ruinen (1938) wrote "Kernbilder" (nuclear pictures [plural]), that is, it is not known whether this figure shows two nuclear apparatuses with each two macronuclear nodules or a single nuclear apparatus with four nodules. **l1, l4:** *Cladotricha koltzowii* variety *gigas*. **l2, l3:** *Cladotricha koltzowii* forma *typika*. AZM = adoral zone of membranelles, FC = frontal cirrus, FVR = long frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RE = replication band, RMR = right marginal row. Page 242.

able, that is, composed of two or four macronuclear nodules with micronuclei attached at different positions. Presence/absence of contractile vacuole and cortical granules not described. Adoral zone more or less gonostomatid, that is, distal end not extending posteriorly on right side; distalmost two membranelles rather large, middle portion of zone (about 15 membranelles) runs along left cell margin, and proximal part (about 10 membranelles) turns obliquely backwards towards cell midline. For variability of frontal ciliature, see Fig. 43j, k (see remarks); details should not be overinterpreted. Usually one short frontoventral row composed of 4–6 cirri left of anterior portion of long frontoventral row. Long frontoventral row parallel to right marginal row, commences close to distal end of adoral zone, composed of about 23 cirri in specimen illustrated, distinctly shortened posteriorly (Fig. 43k); sometimes two long frontoventral rows present (Fig. 43j). Transverse cirri lacking. Marginal rows extend towards rear cell end. For some generic features described by Ruinen (1938), see remarks at genus section.

Population described by Borror & Evans (1979): Body size not indicated; prepared specimen (protargol impregnation?) illustrated 87 × 17 µm (Fig. 43m). Two or four elongate macronuclear nodules serially arranged in midline. Micronuclei not described. Presence/absence of contractile vacuole and cortical granules not mentioned, movement not described. Adoral zone of specimen illustrated occupies 31% of body length (Fig. 43m), composed of about 26 membranelles. Anteriormost/distalmost three membranelles relatively massive, arranged, as is usual, on dorsal side of frontal scutum. Remaining membranelles composed of one short and two long rows of cilia. Undulating membranes closely arranged in parallel, slightly shifted longitudinally; not distinctly gonostomatid. Specimen illustrated with two slightly enlarged frontal cirri, likely the left and middle cirrus; obviously they are arranged in the *Gonostomum* pattern, that is, left cirrus distinctly displaced posteriad; buccal cirrus obviously lacking; one short cirral row (parabuccal row) composed of six cirri extends from distal end of adoral zone to about level of anterior end of undulating membranes.[1] Cirral rows slightly twisted. Long frontoventral row commences, like right marginal row, dorsolaterally close to anterior body end, composed of about 35 cirri, terminates at 81% of body length in specimen illustrated. Transverse cirri absent. 1–4 right marginal rows; in specimen illustrated single right marginal row composed of about 38 cirri and slightly shortened posteriorly. Invariably (n not given) one left marginal row, commences behind buccal vertex, extends to rear cell end, composed of about 28 cirri (estimated from Fig. 43m); cirri composed of three cilia only. Dorsal infraciliature neither described nor illustrated.

Cell division (Fig. 43n–s): This part of the life cycle was described by Borror & Evans (1979) for the Great Salt Lake population (for summaries, see Borror 1979a, Borror & Wicklow 1982, and Foissner 1996, p. 105). The oral primordium originates epiapokinetally in the postoral region (Fig. 43n). The formation of membran-

[1] According to Borror & Evans (1979) "frontal cirri are in 2 groups; one longitudinal-oblique row of 5–8 cirri lies parallel to the right marginal, and 2–5 additional cirri are grouped at the extreme anterior end of the ventral surface."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elles commences, as is usual, in the anterior portion of the primordium (Fig. 43o–q). On the right side of the oral primordium the long undulating membrane anlage and a short streak are formed (Fig. 43o, p). Somewhat later a further short streak, obviously anlage III for the parabuccal row, is present (Fig. 43q). Unfortunately, no comments have been made about the exact origin (de novo? from oral primordium?). In the proter one or two short anlagen originate, likely de novo (Fig. 43p), although in a somewhat later divider (Fig. 43q) these anlagen are lacking. In a middle to late divider the left frontal cirrus, the undulating membranes, and the anterior portion of the short frontoventral row are dedifferentiated to anlagen (Fig. 43r); in addition, the de novo(?) anlage already present in an early divider (Fig. 43p) is again present. Within the long frontoventral row two long anlagen, one for the proter and one for the opisthe, are recognisable (Fig. 43r). In the opisthe of the specimens shown in Fig. 43r, s, a short anlage right of the anterior portion of the long frontoventral row anlage is recognisable; its origin and designation are not explained by Borror & Evans (1979). The marginal rows originate in the ordinary manner, that is, two anlagen occur within each parental row. The parental adoral zone is retained for the proter. All parental cirri are resorbed. The ontogenesis of the dorsal infraciliature is not described. The population studied by Borror & Evans (1979) reproduced relatively slowly, that is, made less than one fission per day. According to Gaievskaïa (1925, p. 264), division occurs preferable at a salt content of 90–160‰.

Resting cyst (Fig. 43i): Cyst globular, with two resistant, refractive layers, which are preserved for 3–4 months after excystment. Diameter of cyst about 24 µm (Gaievskaïa 1925).

Occurrence and ecology: *Cladotricha koltzowii* is very likely confined to saline to highly saline (hypersaline) habitats (e.g., salt lakes) mainly at 20–230‰ salt content; tolerates somewhat more in experiments in anabiotic condition. The records substantiated by morphological data are from the Black Sea area, Portugal, Australia, and North America. Type locality is Lake Solenoïté (Solenoje) near Sevastopol, a port city in Ukraine, located on the south-west coast of the Crimean peninsula (Black Sea; Gaievskaïa 1925). Unfortunately, I could not find the lake in various maps so that it cannot be excluded that it does no longer exist. Ruinen (1938)

← **Fig. 43m–s** *Cladotricha koltzowii* (from Borror & Evans 1979. Protargol impregnation?). **m:** Infraciliature of ventral side and nuclear apparatus of non-divider, 87 µm. Note that a buccal cirrus is lacking. **n–s:** Infraciliature of ventral side of dividers (s = 82 µm; other specimens likely drawn to scale). Broken lines connect cirri originating from same anlage (only shown for anlagen I–III); supposed frontal cirri connected by dotted lines in (m) and (s). **n:** The oral primordium originates epiapokinetally. **o:** The adoral membranelles and the undulating membrane anlage of the opisthe begin to form. **p:** Each one anlage (likely II) is formed (de novo?) in both the proter and the opisthe (arrows). **q:** Middle divider with anlagen I (long arrow), II (middle arrow), and III (short arrow) in opisthe. No anlage clearly recognisable in proter. **r, s:** Late and very late divider. Note that right of the anterior portion of the long frontoventral row a short (additional?) row is present (asterisks); its origin (de novo?) is not described. AZM = adoral zone of membranelles of proter (parental) and opisthe (new), FVR = long frontoventral row, LMR = left marginal row of proter, MA = macronuclear nodule, OP = oral primordium, RMR = right marginal row, I–III = cirri/cirral rows/anlagen. Page 242.

found *C. koltzowii* at salt concentrations from 160‰ to saturation in sample(s) from (i) a saline in Setubal, a city about 30 km south-east of Lisbon (Portugal); (ii) "Voigt", which is, according to Ruinen (1938, p. 246), a gypsum or salt lake in southern Australia; and (iii) Marion Bay, southern Australia. Borror & Evans (1979) recorded *C. koltzowii* and *C. variabilis* (now *Apourosomoida variabilis*) along the southern and eastern beaches of the Great Salt Lake, Utah, USA with salt concentrations from 200‰ to only 10‰ near the mouth of the Jordan River.

Records not substantiated by morphological data: Isla, a beach at the inner end of the estuary Cabo Quejo, Bay of Biscay (Atlantic Ocean), Spain (Fernandez-Leborans & Novillo 1993, p. 216; 1994a, p. 27); saline lake in the Kruglaja Bay near Sevastopol, Crimea peninsula, Ukraine (Dagajeva 1930, p. 35); psammon and ultrahaline water bodies (150–250‰) of Caspian Sea (Agamaliev 1967, p. 1427; 1969, p. 959); benthic in the Bol'shoy Kyzylachag Bay (salinity about 12‰), Kizkyar Bay (salinity about 100‰), and other areas of the Caspian Sea (Agamaliyev 1974, p. 21; Agamaliev 1967a, p. 369; 1983, p. 36; 1990, p. 61); ultrahaline (200–350‰) lakes Kyurdakhany and Masazyr, Apsheron Peninsula, Azerbaijan (Agamaliev 1980, p. 336; as *Strongylidium koltzowii*); at 56–206‰ in a solar saltern in Hwasung, the Korean coastal area of the Yellow Sea (Lei et al. 2009, p. 310). The record from the River Enza (a southern tributary of the River Po) in the village of Coenzo by Madoni (2005, p. 59) is very likely a misidentification because it is very unlikely that such a highly specialised organism occurs in freshwater.

Gaievskaïa (1925) made experiments with varying salt concentrations. Kolkwitz (1950, p. 56) classified *C. koltzowii* as oligosaprobic indicator of (salt) water quality tolerating a salt concentration of up to 200‰.

Cladotricha koltzowii is omnivorous according to Gaievskaïa (1925, p. 264), that is, feeds on bacteria, small algae, flagellates, and debris. According to Borror & Evans (1979), *C. koltzowii* was tolerant to rapid salinity changes, and reacted normally to salt concentrations as low as 20‰. Specimens where cultured in 6.0% (w/v) Osterhout's solution and feed with a halophilic bacterium isolated from the Great Salt Lake.

***Cladotricha sagittata* Ruinen, 1938**
(Fig. 44a)

1938 ***Cladotricha sagittata* nov. spec.** – Ruinen, Zoöl. Meded., Leiden, 20: 250, Fig. 6 (Fig. 44a; original description; very likely no type material available).

1972 ***Cladotricha sagittata* Ruinen, 1938** – Borror, J. Protozool., 19: 18 (generic revision of hypotrichs).

2001 ***Cladotricha sagittata* Ruinen, 1938** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 16 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: No derivation of the species-group name is given in the original description. The name *sagittat·us*, *-a*, *-um* (Latin adjective [m; f; n]; arrow-shaped) likely refers to the slender fusiform body shape, which is reminiscent of a (slender) arrowhead.

Remarks: Hemberger (1982, p. 25) classified *C. sagittata* as junior synonym of *C. koltzowii*. However, according to the original description the type species has invariably two long frontoventral rows (Fig. 43a–h; see also Fig. 43j), whereas the present species has only one (Fig. 44a). Perhaps the specimen/population shown in Fig. 43k and the population described by Borror & Evans (1979) are identical with *C. sagittata*. More populations have to be studied to elucidate the rather tricky situation.

Morphology: Body length 100–160 µm, length: width ratio about 6–7:1 (specimen illustrated ca. 5.6:1; Fig. 44a). Body outline slender fusiform, anterior end broadly, rear end narrowly rounded. Two elongate macronuclear nodules in central body portion left of midline; two small, globular micronuclei. Contractile vacuole and cortical granules neither mentioned nor illustrated, indicating that they are lacking. Cytoplasm vacuolised. Adoral zone obviously gonostomatid, occupies 28% of body length in specimen illustrated. Distalmost three membranelles enlarged; proximal-most 10 membranelles almost completely covered by buccal lip. Undulating membranes neither illustrated nor mentioned, indicating that they are inconspicuous (gonostomatid?). Cirral pattern of specimen illustrated as follows: two cirri close to frontal scutum (probably the middle and right frontal cirrus); two rather strong cirri close to left anterior portion of adoral zone, likely the anterior one is the left frontal cirrus which is distinctly displaced posteriad in gonostomatids (the rear one is perhaps the buccal cirrus); three cirri (parabuccal row?) more or less behind right frontal cirrus; long frontoventral row commences close to distal end of adoral zone, composed of about 18 cirri, terminates somewhat ahead of rear cell end; one distinctly enlarged cirrus in elongation of rear end of long frontoventral row; right marginal row parallel to long frontoventral row, anterior portion likely extending dorsolaterally; left marginal row commences left of buccal vertex, terminates somewhat ahead of rear end. In total three enlarged cirri on rear cell end (including that in the elongation of the long frontoventral row), not spread and thus forming bundle; according to Ruinen (1938), these are caudal

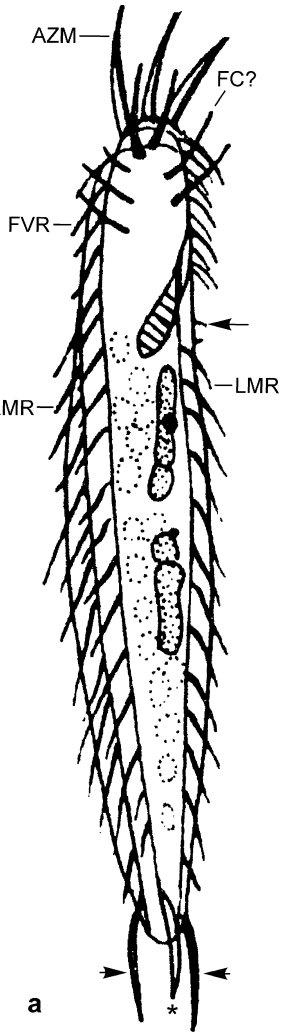


Fig. 44a *Cladotricha sagittata* (from Ruinen 1938. From life). Ventral view, 100–160 µm. Long arrow marks dorsal bristle. The strong cirri at the rear cell end (short arrows and asterisk) are caudal cirri according to Ruinen (1938). However, protargol impregnation is needed for more detailed observations and correct designation of the cirri (details see text). AZM = adoral zone, FC? = left frontal cirrus?, FVR = frontoventral row, LMR = left marginal row, RMR = right marginal row. Page 252.

cirri (of course, details of the cirral pattern have to be confirmed by protargol preparations and ontogenetic data). Dorsal bristles about 5 µm long, kinety pattern not known.

Occurrence and ecology: Likely confined to highly saline waters. Type locality of *Cladotricha sagittata* is Madura Island (north-west of Bali), Indonesia, where Ruinen (1938) discovered it in samples with 30–60‰ NaCl. No further records published. Food not known.

Cladotricha sigmoidea Ruinen, 1938
(Fig. 45a–f)

1938 ***Cladotricha sigmoidea* nov. spec.** – Ruinen, Zoöl. Meded., Leiden, 20: 251, Fig. 7 (Fig. 45a–f; original description; very likely no type material available).
1972 ***Cladotricha sigmoidea* Ruinen, 1938** – Borror, J. Protozool., 19: 18 (generic revision of hypotrichs).
1983 ***Cladotricha sigmoidea*** – Post, Borowitzka, Borowitzka, Mackay & Moulton, Hydrobiologia, 105: 102, Fig. 14 (record from Australia substantiated by photomicrograph).
2001 ***Cladotricha sigmoidea* Ruinen, 1938** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 16 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: No derivation of the species-group name is given in the original description. The name *sigmoide·us, -a, -um* (Latin adjective [m; f; n]; sigmoidal, half-moon-shaped) obviously alludes to the slightly helically curved body.

Remarks: This is the smallest species described by Ruinen (1938). According to Borror (1972) it is a valid species of uncertain systematic position. Hemberger (1982, p. 25) classified it, like *C. sagittata*, as junior synonym of *C. koltzowii*. The micrograph provided by Post et al. (1983) is indeed reminiscent of *C. sigmoidea*, indicating that is a valid species.

When I made the key to *Cladotricha* I could not find a good distinctive feature for *C. sigmoidea* and *Uroleptus packii*, except of the pale green colour of the latter, which is very likely due to symbiotic algae. Thus, synonymy of these two species cannot be excluded. However, a definite synonymy would require a combination of *U. packii* with *Cladotricha*, supposed that the classification in *Cladotricha* is correct at all. Since detailed data are lacking for both species, which are from rather distant localities (a salt lake in southern Australia and the Great Salt Lake in USA), I preliminary refrain from such an act and review *U. packii* (as *Strongylidium packii*) as incertae sedis in *Cladotricha*. Further populations have to be studied to provide a refined classification.

Morphology: The following characterisation is solely based on the original description, because Post et el. (1983) did not provide details, except the body length (59 µm) of the specimen photographed. Values deduced from Fig. 45a must not be overinterpreted.

Body length 60–80 µm, length:width ratio of specimen illustrated about 4.2:1 (Fig. 45a). Body broadly fusiform, sigmoidal and slightly twisted about main body axis; anterior end broadly, rear end narrowly rounded; dorsoventrally flattened. Two globular or ellipsoidal macronuclear nodules in central body portion slightly left of

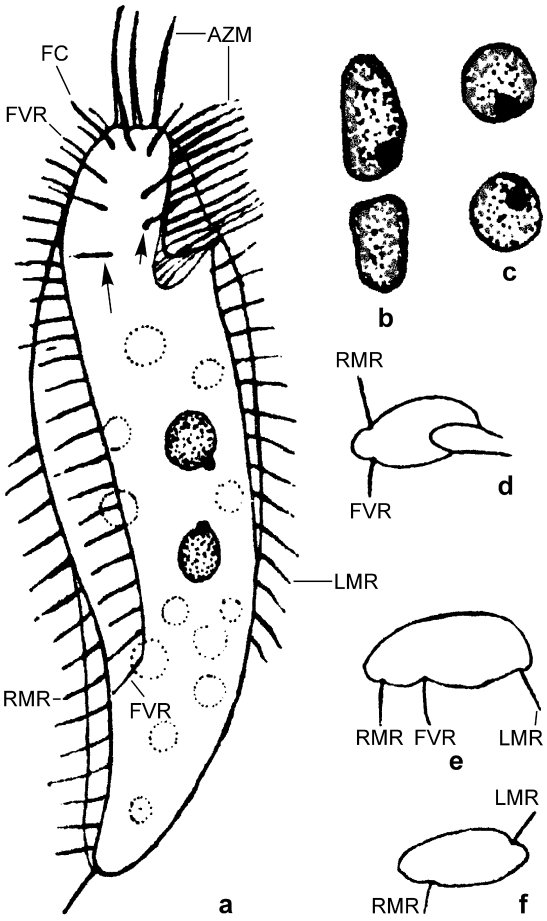


Fig. 45a–f *Cladotricha sigmoidea* (from Ruinen 1938. From life). **a:** Ventral view showing, inter alia, sigmoidal body, 60 to 80 µm. Short arrow marks buccal(?) row, long arrow denotes parabuccal(?) row. **b, c:** Ellipsoidal and globular macronuclear nodules (with attached micronuclei). **d–f:** Cross sections (in the front, at centre, in the back) showing course of cirral rows and dorsoventral flattening. AZM = adoral zone of membranelles, FC = right frontal cirrus, FVR = long frontoventral row, LMR = left marginal row, RMR = right marginal row. Page 254.

midline; each one small, globular micronucleus attached. Contractile vacuole and cortical granules neither illustrated nor mentioned, indicating that they are lacking. Cytoplasm strongly vacuolised. Adoral zone occupies 17–25% of body length, composed of three large frontal and about 14 proximal membranelles (values from Fig. 45a); bases of proximal membranelles rather wide. Undulating membranes neither mentioned nor illustrated. Three frontal cirri; specimen illustrated with two (buccal?) cirri close to proximal portion of adoral zone and three (parabuccal?) cirri behind right frontal cirrus. According to Ruinen (1938), cirral pattern of frontal field typical, "sometimes a row of five cirri behind the front three". Long frontoventral row commencing close to distal end of adoral zone, sigmoidally extending into rear body third, terminating at 72% of body length and composed of 26 cirri in specimen illustrated (Fig. 45a). Right marginal row commences on dorsal side, extends sigmoidally to rear cell end; left row begins left of buccal vertex, extends dorsolaterally in rear body portion. Dorsal ciliature not known.

Occurrence and ecology: *Cladotricha sigmoidea* is likely confined to highly saline habitats. It was discovered in a 160‰ NaCl solution from "Voigt", which is, according to Ruinen (1938, p. 246), a gypsum or salt lake in southern Australia. Records not substantiated by morphological data: shallow, saline pans in the National Park Neusieldersee/Seewinkel, Burgenland, Austria (Zimmermann-Timm & Herzig 2006, p. 1945); Hutt Lagoon (28°11' S 114°15'E), about 600 km north of Perth, Australia (Post et al. 1983; with photomicrograph, see remarks). A voracious consumer of *Dunaliella* according to Post et al. (1983).

Cladotricha spec. in Nießen (1984)
(Fig. 46a–r, Table 19)

1984 ***Cladotricha* nov. spec.** – Nießen, Diploma thesis, p. 52, Abb. 15a–j, Table on p. 52 (Fig. 46a–r; description; slides likely deposited in the University of Bonn, Germany).

Nomenclature: Note that this is a nomenclaturally invalid publication, inter alia, because no species-group name was proposed.

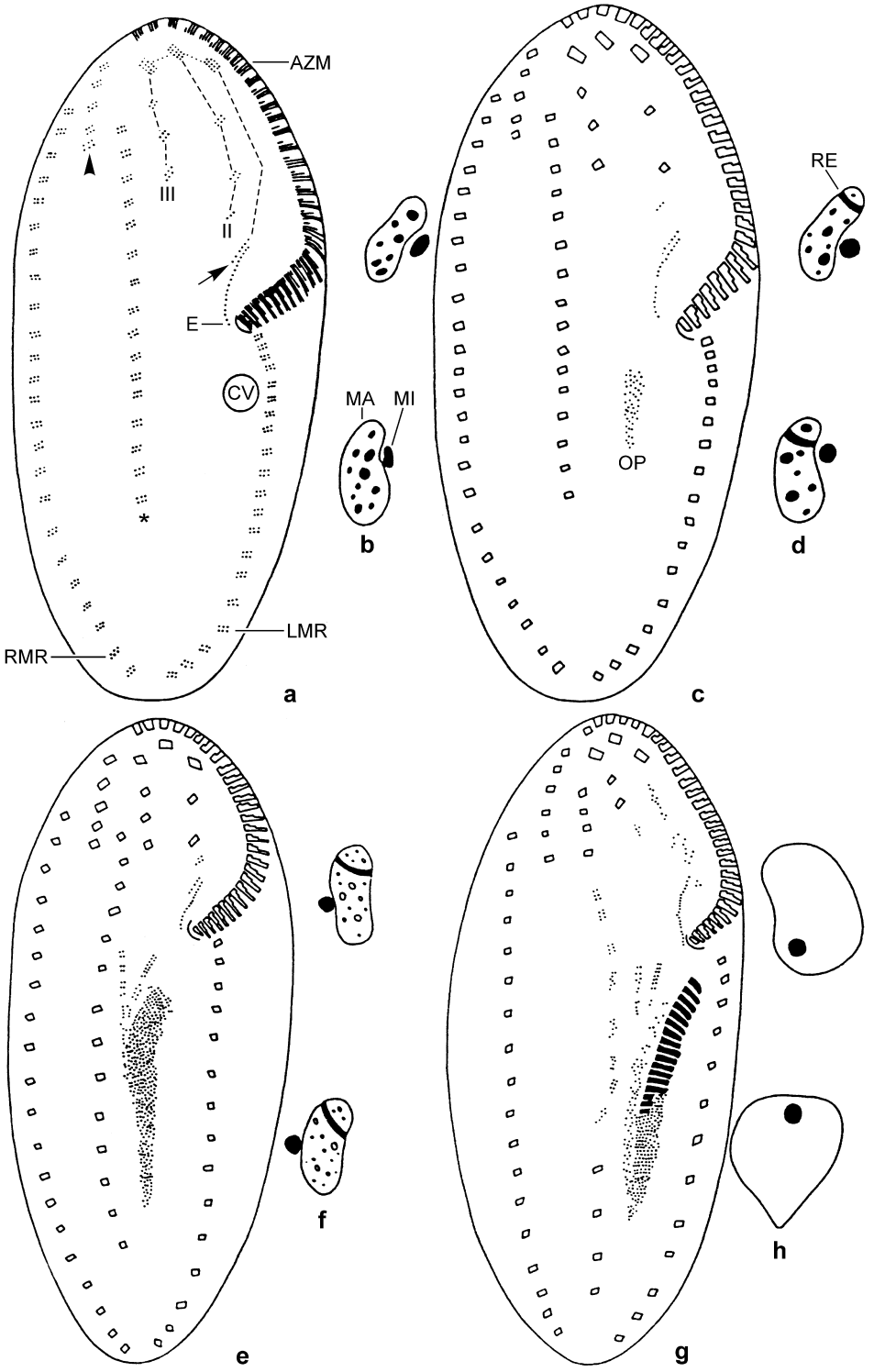
Remarks: Nießen (1984), who made her thesis at the University of Bonn likely under the supervision of N. Wilbert, found this population during the investigation of saline soils from various localities. Unfortunately, neither Nießen (1984) nor Wilbert (1995) – who validly published two other *Cladotricha* species described in the thesis – mentioned the exact sample site of this population (further details see occurrence and ecology). Nießen (1984) provided no illustration of a live specimen, but listed some features studied in vivo.

The ventral and dorsal infraciliature agree almost perfectly with that of *C. edaphoni* Wilbert, 1995, a junior synonym of *C. australis*. However, the different number of macronuclear nodules (two vs. many; Table 19) prove that synonymy can be excluded. Perhaps it is identical with *C. sigmoidea* which was discovered in South Australia, where Nießen (1984) collected the main portion of her soil samples (see below).

The anlagen for the right frontoventral row originate de novo (Fig. 46k), obviously due to the brevity of the row. By contrast, in *C. halophila*, which has a long right frontoventral row, the two anlagen originate within the parental row (Fig. 49i, k).

Morphology: Body size in protargol preparations 108 × 45 µm on average (Table 19; Wilbert-method), length:width ratio almost 2:1. Two macronuclear nodules;

Fig. 46a–h "*Cladotricha* nov. spec." in Nießen (1984) (from Nießen 1984. Protargol impregnation). **a, b:** → Infraciliature of ventral side and nuclear apparatus, 120 µm. Arrowhead marks end of right frontoventral row, asterisk marks end of left frontoventral row. Long arrow denotes paroral. Cirri originating from the same anlage are connected by broken line (only shown for anlagen I–III). Frontal cirri connected by dotted line. **c–h:** Infraciliature of ventral side and nuclear apparatus of very early, early, and middle divider (details see text). AZM = adoral zone of membranelles, CV = contractile vacuole, E = endoral, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, OP = oral primordium, RE = replication band, RMR = right marginal row, II, III = cirral row/anlagen. Page 256.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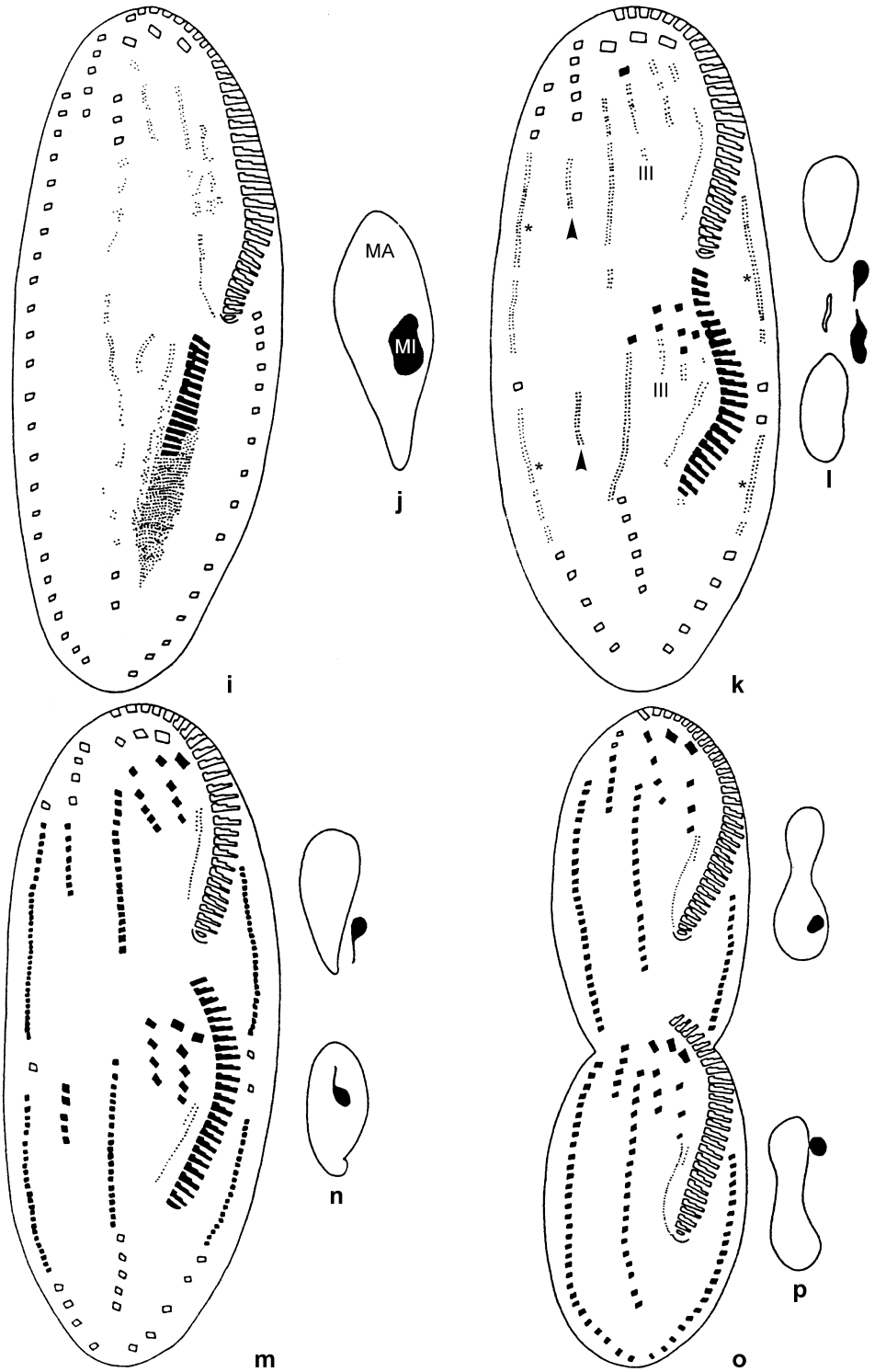
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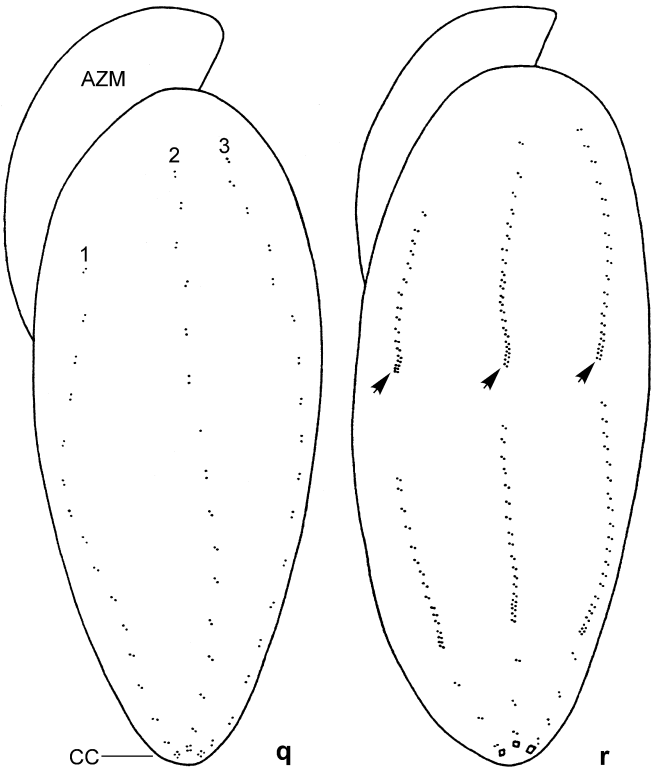


Fig. 46q, r "*Cladotricha* nov. spec." in Nießen (1984) (from Nießen 1984. Protargol impregnation). **q:** Infraciliature of dorsal side of interphasic specimen. **r:** Morphogenesis of dorsal side. Arrows mark caudal cirri of proter. AZM = adoral zone of membranelles, CC = caudal cirri, 1–3 = dorsal kineties. Page 256.

to each nodule one micronucleus attached. Presence/absence of cortical granules not mentioned. Contractile vacuole slightly behind buccal vertex. Movement slow, spirals about main body axis.

Adoral zone gonostomatid, occupies 47% of body length and composed of 31 membranelles on average. Undulating membranes also gonostomatid, that is, paroral composed of few (about six) cilia, arranged more or less in parallel to anterior portion of endoral, which ends at buccal vertex.

Three slightly enlarged frontal cirri arranged in somewhat curved pseudorow, that is, left cirrus not distinctly displaced posteriad. Specimen illustrated with buccal row composed of three cirri, rearmost one consisting of only one kinety (Fig. 46a). Behind right frontal cirrus three parabuccal cirri. Left frontoventral row slightly shorted anteriorly, terminates at 71% of body length in specimen illustrated (Fig. 46a). Right frontoventral row short, commences about at level of frontal cirri, terminates about at same level as parabuccal row. Transverse cirri lacking. Right marginal

← **Fig. 46i–p** "*Cladotricha* nov. spec." in Nießen (1984) (from Nießen 1984. Protargol impregnation). Middle, late, and very late dividers. Arrowheads in (k) mark the de novo formation of the right frontoventral row, the asterisks denote the marginal row anlagen. Parental cirri white, new black. MA = fused macronucleus, MI = micronucleus, III = cirral anlage III. Page 256.

row shortened anteriorly, terminates, like left row, close to rear cell end, that is, marginal rows only inconspicuously separated posteriorly. Left marginal row commences close to buccal vertex, cirri anteriorly more closely spaced than posteriorly. Most cirri composed of 2 × 3 cilia; marginal cirri about 10 µm long.

Dorsal bristles about 2 µm long, arranged in three kineties; kinety 1 distinctly shortened anteriorly. One about 8 µm long caudal cirrus on rear end of each kinety (Fig. 46q).

Cell division (Fig. 46c–p, r): This part of the life cycle is described by Nießen (1984). The morphogenesis commences with the de novo formation of an oral primordium in the postoral area (Fig. 46c). The oral primordium becomes larger and two anlagen extending anteriorly are formed (Fig. 46e). When the anterior half of the oral primordium is modified to membranelles, some loosely arranged basal bodies close to the right margin of the oral primordium are recognisable – the undulating membrane anlage for the opisthe. The anlagen II and III become more distinct and the cirri of the middle portion of the left frontoventral row are modified to a long primary(?) primordium. In addition, the parental undulating membranes, the buccal cirri, and the rearmost parabuccal cirrus disorganise (Fig. 46g). In the specimen shown in Fig. 46i, all buccal and parabuccal cirri have modified to proter's anlagen II and III, respectively. The parental undulating membranes also have disorganised, but it is ambiguous how anlage I exactly originates (de novo? from disorganised parental undulating membranes? from buccal row?). Somewhat later, the anlagen for the right frontoventral row originate de novo between the right marginal row anlagen and the anlagen for the left frontoventral row (Fig. 46k). In later stages the differentiation of cirri continues and the individual parts of the infraciliature migrate to their final positions (Fig. 46m, o). The parental adoral zone is retained for the proter.

Dorsal kineties divide in the plesiomorphic *Gonostomum*-pattern, that is, within each kinety two anlagen occur, the anterior for the proter and the posterior for the opisthe. Caudal cirri are formed at the rear end of each kinety (Fig. 46r).

The nuclear apparatus divides in the ordinary way, that is, replication bands occur in the macronuclear nodules, which fuse to a single mass, and later divide into the species-specific number (Fig. 46b, d, f, h, j, l, n, p).

Occurrence and ecology: Likely confined to highly saline habitats. Unfortunately, Nießen (1984) did not mention the sample site. She collected saline soils (depth 0–10 cm) at various sites in the Coorong National Park and the Murray River System in South Australia, but also from the marginal area of the Birket el Qarum, a sodium lake near El Fayum in Egypt. Nießen (1984) cultured the specimens at salinities of 32–60‰ and pH 8.8. Feeds on bacteria (Nießen 1984).

Cladotricha spec. in Nießen (1984)
(Fig. 47a–d)

1984 ***Cladotricha* spec.** – Nießen, Diploma thesis, p. 68, Abb. 18a, b (Fig. 47a–d; description; slides likely deposited in the University of Bonn, Germany).

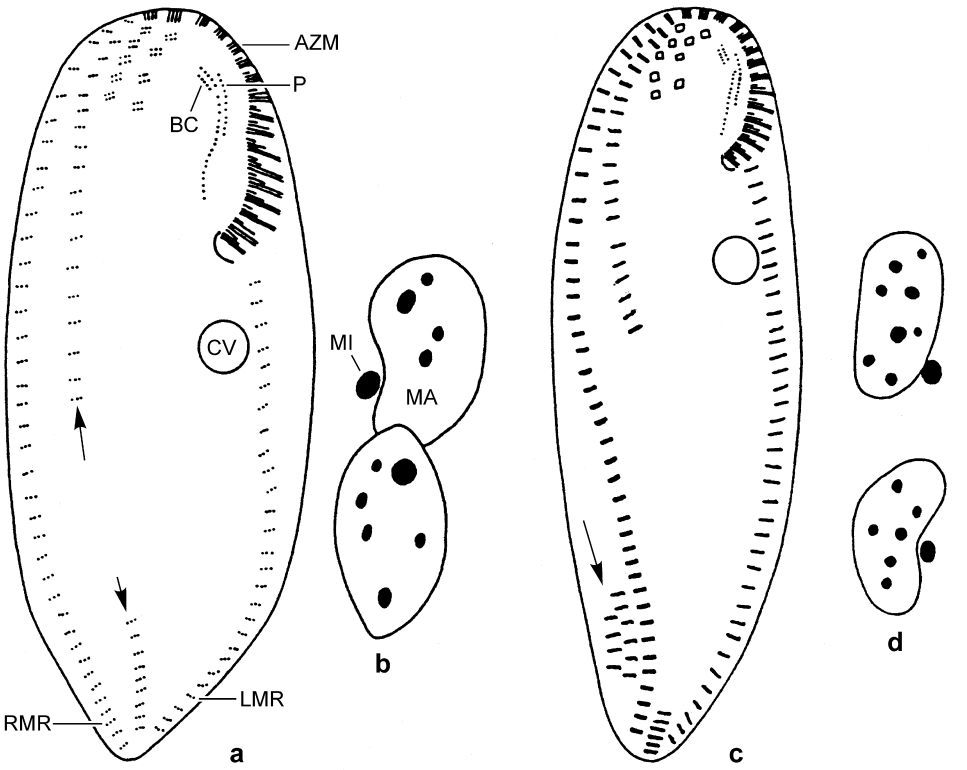


Fig. 47a–d *Cladotricha* spec. in Nießen (1984) (from Nießen 1984. Protargol impregnation). **a, b:** Infraciliature of ventral side and nuclear apparatus, 90 µm. Long arrow marks frontoventral row, short arrow denotes cirral row between rear portion of marginal rows (whether this row is formed by the same anlage as the long frontoventral row or not is not known). Note that most cirri are composed of a single kinety only. The cirral pattern of the frontal region is difficult to interpret. **c, d:** Infraciliature of ventral side and nuclear apparatus of specimen with some extra cirri (arrow; not resorbed parental cirri?). AZM = adoral zone of membranelles, BC = buccal cirrus, CV = contractile vacuole, LMR = left marginal row, MA = macronuclear nodule, Mi = micronucleus, P = paroral, RMR = right marginal row. Page 260.

Nomenclature: Note that this is a nomenclaturally invalid publication, inter alia, because no species-group name was proposed.

Remarks: See first paragraph at "*Cladotricha* spec. in Nießen (1984)" (p. 256). The description contains some irregularities, for example, according to the text the basal bodies of the undulating membranes are zigzagging, whereas they form straight lines in the illustrations. Nießen (1984) classified this unpublished species preliminary in *Cladotricha* because the frontal cirri are arranged in two groups and one ventral row is present. She correctly stated that the final classification needs cell division data, which, inter alia, will explain the origin of the short cirral row in the posterior body portion.

Morphology: Body size in life(?) 70–110 × 25–35 µm; length:width ratio 2:1. Body outline in life(?) wide oval, anterior end broadly rounded, posterior portion slightly tapered. Body very flexible. Two ellipsoidal, wide spindle-shaped, or reniform macronuclear nodules; one roughly globular micronucleus attached to each macronuclear nodule. Contractile vacuole somewhat behind buccal vertex, that is, slightly displaced inwards. Presence/absence of cortical granules not mentioned. Cytoplasm with many small inclusions, especially in posterior body portion, which is thus dark at low magnification. Adoral zone occupies 21% (Fig. 47c), respectively, 33% (Fig. 47a) of body length in specimens illustrated; zone composed of only 13–15 membranelles according to the text, but of 15–17 according to the illustrations; adoral zone gonostomatid. Undulating membranes straight to slightly curved, paroral(?) commences more anteriorly than endoral(?), membranes roughly arranged in parallel and composed of linearly arranged basal bodies (see remarks). Buccal cirrus right of anterior end of paroral, slightly larger than cirri of short frontoventral rows, which are composed of four or five cirri each. Long frontoventral row commences close to distal end of adoral zone, terminates roughly in mid-body and composed of about 17–19 cirri. A row of about 6–9 cirri in median of rear body portion, separating marginal rows more or less distinctly (note that these are not transverse cirri). Right marginal row composed of 38–42 cirri, begins – like long frontoventral row – near adoral zone, terminates at rear cell end. Left marginal row composed of 27–37 cirri, begins near buccal vertex, terminates about at same level as right row. One specimen with two short cirral rows right of posterior portion of right marginal row, according to Nießen (1984) unresorbed parental cirri. Cirri of long frontoventral row, ventral cirri close to posterior end, and marginal cirri composed of single kinety only. Cirri about 8–9 µm long. On the dorsal side, Nießen (1984) could only recognise some irregularly arranged basal body pairs.

Occurrence and ecology: Unfortunately, Nießen (1984) did not mention the sample site. She collected saline soils (0–10 cm) at various sites in the Coorong National Park and the Murray River System in South Australia, but also from the marginal area of the Birket el Qarum, a sodium lake near El Fayum in Egypt. Both specimens illustrated are, however, from the same sample site with 39‰ salt content and pH 8.6. Short-lived, that is, three days after excystment active specimens disappeared from culture. Difficult to impregnate.

Cladotricha australis Blatterer & Foissner, 1988
(Fig. 48a–l, Table 19)

1984 ***Cladotricha* spec.** – Nießen, Diploma thesis, p. 66, Abb. 17a, b, Table on p. 66 (Fig. 48i–l; description of morphology of synonym *C. edaphoni*; see nomenclature).

1988 ***Cladotricha australis* nov. spec.**[1] – Blatterer & Foissner, Stapfia, 17: 32, Abb. 9a–h, Tabelle 7 (Fig. 48a–h; original description; the holotype slide [accession number 1989/53] and one paratype slide [1989/54] have been deposited in the Upper Austrian Museum in Linz [LI]; Aescht 2008, p. 145).

[1] Blatterer & Foissner (1988) provided the following diagnosis: In vivo etwa 90–130 × 25–35 µm große

1995 ***Cladotricha edaphoni* sp. n.**[1] – Wilbert, Acta Protozool., 34: 277, Fig. 10a–c, Table 10 (Fig. 48i–l; new synonym; the type material is deposited in the Zoological Institute of the University of Bonn [Poppelsdorfer Schloß], Germany).

2001 ***Cladotricha australis* Blatterer and Foissner, 1988** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 15 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: No derivation of the species-group names is given in the original descriptions. The name *australis* (Latin; southern, austral) refers to the country/continent (Australia) where the species was discovered. The species-group name *edaphoni* (from *edaphon*; Greek noun; the soil flora and fauna) refers to the habitat (soil) where the junior synonym was discovered.

This species was first described, but nomenclaturally not validly published (no species-group name assigned, thesis paper) by Nießen (1984). Eleven years later, Wilbert – who was very likely the supervisor of the thesis – provided the valid publication (Wilbert 1995) of the population studied by Nießen (1984). Since Nießen is not mentioned in the original description, Wilbert is deemed to be the author of *C. edaphoni* (ICZN 1999, Article 50.1.1). Blatterer & Foissner (1988, p. 2) mentioned the paper by Nießen (1984), but did not discuss the work in the species comparison.

Remarks: Blatterer & Foissner (1988) discovered *C. australis* in saline soil close to Lake Alexandria near Adelaide, Australia. The synonym *C. edaphoni* and *C. halophila*, which is perhaps a further synonym (see below), were isolated from the same area (Coorong National Park near Adelaide). The same type locality and basically the same morphology strongly indicate, actually prove, that *C. australis* and *C. edaphoni* are synonyms. Wilbert (1995), who collected the sample in January 1986, did not know the paper by Blatterer & Foissner (1988), who sampled in October and November 1986 and February 1987. The only noteworthy difference is in the length of the right frontoventral row (terminates far behind level of buccal vertex in *C. australis* vs. about at level of buccal vertex in *C. edaphoni*).

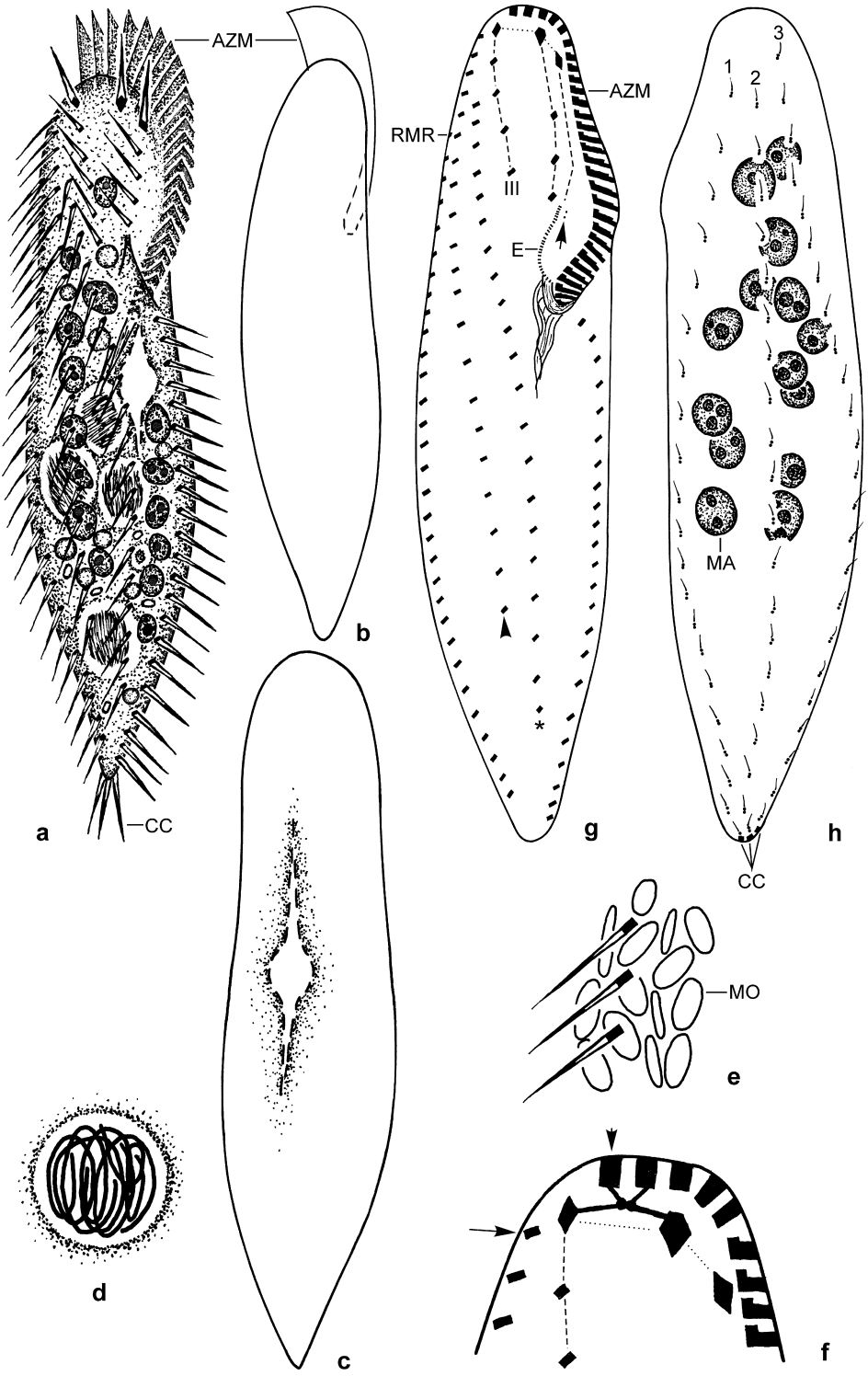
Cladotricha halophila is perhaps a further junior synonym of *C. australis*. Preliminary I keep them separate because there are two differences, which are, however, diagnostically not very conclusive: the number of buccal cirri (1 in *C. halophila* vs. 1–5, 3.3 on average) and the number of macronuclear nodules (5–14, 9.6 on average vs. 13–28, 18.4; Table 19). Further populations from this area have to be studied to demonstrate whether or not these differences are stable.

A synonymy of *C. australis* and *Neowallackia franzi* (p. 281) can be excluded because caudal cirri are lacking in this Eurasian species inhabiting non-saline soils.

Neowallackia ghangriai has caudal cirri, according to the original description (p. 295). However, these "caudal" cirri are the misinterpreted rearmost cirri of the left marginal row. In addition, *N. ghangriai* has cortical granules and extrusomes so that a synonymy with *C. australis* can be excluded.

Cladotricha mit durchschnittlich 25 adoralen Membranellen, 18 Makronucleus-Teilen, 2 langen Ventralreihen und 2 kurzen frontalen Cirrenreihen. 3 Dorsalkineten.

[1] Wilbert (1995) provided the following diagnosis: In vivo 90–125 × 32–49 µm *Cladotricha*, shaped like a slender spindle with 15–20 macronuclear segments, 2 ventral rows, 3 dorsal kineties and 3 caudal cirri.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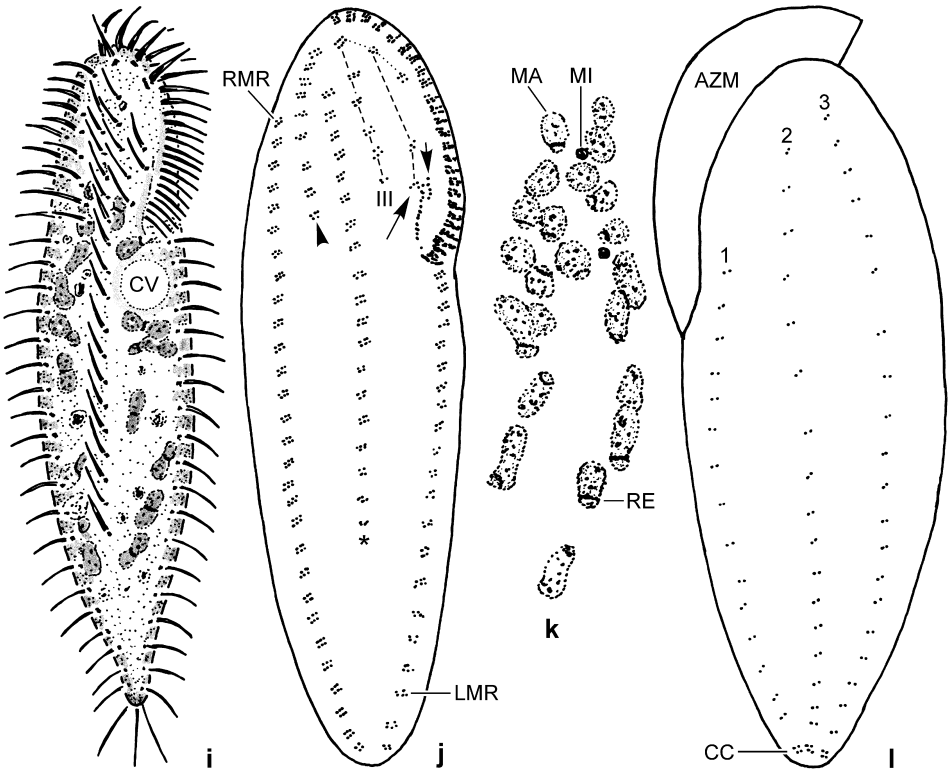

Fig. 48i–l *Cladotricha australis* (the new synonym *C. edaphoni*, after Wilbert 1995. i, from life; j–l, protargol impregnation). **i:** Ventral view, about 130 µm. **j, k:** Infraciliature of ventral side and nuclear apparatus, 122 µm. The illustrations in the original description are so tiny that they could not be used; therefore sophisticated details (e.g., exact number and arrangement of basal bodies within cirri) in the redrawings must not be overinterpreted (for better illustrations, see Nießen 1984). Short arrow marks paroral, long arrow denotes rearmost buccal cirrus; asterisk marks left frontoventral row, arrowhead denotes rear end of right frontoventral row. Frontal cirri connected by dotted line, broken lines connect cirri originating from same anlage (only shown for anlagen II, III). **l:** Infraciliature of dorsal side, 107 µm. AZM = adoral zone of membranelles, CC = caudal cirri, CV = contractile vacuole, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RE = replication band, RMR = anterior end of right marginal row, III = frontoventral cirral row III (right frontal cirrus and parabuccal cirri), 1–3 = dorsal kineties. Page 262.

← **Fig. 48a–h** *Cladotricha australis* (from Blatterer & Foissner 1988. a–e, from life; f–h, protargol impregnation). **a:** Ventral view of representative specimen, 129 µm. **b, c:** Shape variants in ventral and dorsal view showing adoral zone and contractile vacuole with collecting canals. **d:** Food vacuole with bundled bacteria. **e:** Mitochondria underneath cell surface in top view. **f:** Frontal ciliature at high magnification showing x-shaped fibres connecting right and middle frontal cirrus and two distalmost membranelles. Short arrow marks distal end of adoral zone, long arrow denotes anterior end of right frontoventral row. Frontal cirri are connected by dotted line. **g, h:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 102 µm. Arrow marks very short paroral (two cilia!), arrowhead denotes right frontoventral row; asterisk denotes rear end of left frontoventral row. Broken lines connect cirri originating from same anlage (only shown for anlagen I–III), dotted line connects frontal cirri, which are arranged in the characteristic *Gonostomum*-pattern. AZM = adoral zone of membranelles, CC = caudal cirri, E = endoral, MA = macronuclear nodule, MO = mitochondrium(?) close beneath cell surface, RMR = anterior end of right marginal row, III = frontoventral cirral row III (right frontal cirrus and parabuccal cirri), 1–3 = dorsal kineties. Page 262.

Morphology: Although the synonymy is beyond reasonable doubt, I keep the two descriptions separate, so that even workers which do not agree with the synonymy can use the revision. At first the population investigated by Blatterer & Foissner (1988) is described.

Body size of population studied by Blatterer & Foissner (1988) in life 90–130 × 25–35 µm; 91 × 25 µm, that is, length:width ratio 3.6:1 on average in protargol preparations (Table 19). Body outline lanceolate, widest usually at beginning of posterior third of body; anterior half slightly narrowed and broadly rounded; rear body portion tapered and sometimes tail-like elongated (Fig. 48a–c). Body not contractile, only slightly flattened dorsoventrally. On average 18 macronuclear nodules, often arranged in two indistinct rows left and right of cell midline; individual nodules spherical or slightly ellipsoidal, often with one large and several small chromatin bodies. Micronuclei difficult to recognise in protargol preparations, morphometric data thus uncertain (Fig. 48a, h, Table 19). Contractile vacuole about in mid-body slightly left of midline, that is, distinctly displaced inwards, during diastole with two collecting canals (Fig. 48a, c). No cortical granules, but – as in *Urosoma* (for review see Berger 1999, p. 396) – ellipsoidal mitochondria rather distinct (Fig. 48e). Cytoplasm colourless, with tuberous crystals and few, small, fatty-shining globules. Food vacuoles with very long bacteria arranged in thick bundles (Fig. 48d). Movement moderately rapid, without peculiarities.

Oral apparatus gonostomatid, that is, adoral zone commences at anterior cell end, extends along left body margin and curves knee-shaped towards midline; on average composed of 24 membranelles, largest one up to 4 µm wide (Fig. 48a, g). Proximal portion of zone covered by small buccal lip. Buccal field narrow, short, and shallow. Undulating membranes of very different length, as is usual for gonostomatids. Paroral usually composed of two (rarely three or four) clearly separated basal bodies/cilia, arranged left of anterior end of endoral in specimen illustrated: endoral distinctly to slightly sigmoidal, terminates close to buccal vertex. Pharyngeal fibres inconspicuous.

Cirral pattern relatively variable, but usually as shown in Fig. 48a, g. Frontal cirri about 14 µm, other cirri about 12 µm long. Three frontal cirri in *Gonostomum* pattern, that is, left cirrus (I/1) distinctly behind level of middle and right frontal cirrus. Middle and right frontal cirrus connected with distalmost two adoral membranelles by X-shaped fibres (Fig. 48f). 1–5, usually three buccal cirri (originating from anlage II)[1], roughly in line with left frontal cirrus, rearmost cirrus at anterior end of undulating membranes. 3–7, usually four parabuccal cirri, that is, like right frontal cirrus originating from anlage III, rearmost cirrus somewhat above level of rearmost buccal cirrus in specimen illustrated (Fig. 48f, g). Left frontoventral row somewhat

[1] Blatterer & Foissner (1988) write that the rearmost cirrus of this row could be a buccal cirrus. I designate all cirri (except the frontal cirrus) originating from anlage II (see *C. halophila* for details on cell division) as buccal cirri, because we actually do not know which of the three cirri shown in Fig. 48g is homologous to the buccal cirrus (II/2) of the 18-cirri hypotrichs (Fig. 2a). Usually, buccal cirrus II/2 is right of the undulating membranes and therefore the assumption of Blatterer & Foissner (1988) could be correct.

shortened anteriorly and – like right frontoventral row – more or less distinctly shortened posteriorly. Transverse cirri lacking[1]. Right marginal row distinctly shortened anteriorly, ends – like left row – slightly subterminally; left marginal row begins left of buccal vertex.

Dorsal bristles in life about 3 µm long, arranged in three bipolar, more or less straight kineties. One out of 15 specimens with a fourth kinety of half body length (likely an additional [short] row or remnant of the previous generation; it is unlikely that this is a dorsomarginal kinety). Each kinety usually ends with a single caudal cirrus; caudal cirri rather distinct in life, but often difficult to recognise in protargol preparations (Fig. 48h); variability rather high (Table 19).

Wilbert (1995) published a rather brief description and tiny illustrations[2] (Fig. 48i–l). Body size in life 90–125 × 32–49 µm; length:width ratio about 3:1. Body outline very "changeable" (Wilbert likely meant variable), slender fusiform, anterior end moderately, rear end very narrowly rounded or even inconspicuously tailed. 15–20 macronuclear nodules roughly O-shaped arranged, that is, mainly along cell margins. "Invariably" (n = 10) four micronuclei (Fig. 48k). Contractile vacuole immediately behind buccal vertex. Cytoplasm light and translucent. Presence/absence of cortical granules and movement not mentioned.

Oral apparatus as described above; occupies 33% of body length and composed of about 21 membranelles on average. Paroral[3] of specimen illustrated composed of five basal bodies/cilia, left of anterior end of slightly curved endoral, which extends to proximal end of adoral zone (Fig. 48j).

Cirral pattern as shown in Fig. 48j. Three enlarged frontal cirri obviously arranged in *Gonostomum*-pattern, that is, left one distinctly behind level of other two cirri. Specimen illustrated obviously with two buccal cirri (rear one right of anterior end of undulating membranes) and five parabuccal cirri. In total these are 10 cirri (3 + 2 + 5), according to the morphometric characterisation, however, only eight or nine "frontal" cirri are present. Left frontoventral row extends roughly along midline into rear third of cell, slightly shortened anteriorly in specimen illustrated. Right frontoventral row commences about at level of right frontal cirrus, terminates roughly about at level of buccal vertex (main difference to the synonym *C. australis*). Right marginal row, as in the synonym *C. australis*, distinctly shortened anteriorly, terminates – like left row – very close to rear cell end. Left marginal row begins at buccal vertex. Marginal cirri about 10 µm long.

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[1] Blatterer & Foissner (1988) write, obviously par lapsus, that the "Frontal cirri and transverse cirri are about 14 µm long". However, neither in the illustration nor in the morphometric characterisation transverse cirri are recognisable. The rearmost cirri of the frontoventral rows are not transverse cirri because they are neither larger nor smaller than the other cirri nor set off.

[2] The illustrations in the original description are so tiny that they could not be used in the present review. Thus, I made redrawings. Somewhat later I saw that the illustrations of *C. edaphoni* have already been published by Nießen (1984).

[3] Wilbert (1995) misnamed – likely par lapsus – the paroral as "adoral membrane" and simultaneously confounded paroral and endoral.

Table 19 Morphometric data on *Cladotricha australis* (aus, from Blatterer & Foissner 1988; eda, synonym *C. edaphoni* from Wilbert 1995), *Cladotricha halophila* (hal, from Wilbert 1995), and *Cladotricha* spec. (spe, population described on p. 52 in Nießen 1984)

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	aus	91.2	90.5	9.3	2.7	10.2	79.0	108.0	12
	eda	114.1	119.0	11.9	–	–	90.0	125.0	10
	hal	138.4	138.0	14.7	–	–	102.0	172.0	17
	spe	107.6	110.0	6.4	1.6	–	99.0	120.0	15
Body, width	aus	25.4	25.0	4.6	1.3	17.9	20.0	38.0	12
	eda	42.2	42.0	6.2	–	–	32.0	49.0	10
	hal[e]	30.0	30.0	4.0	–	–	5.0	39.0	1
	spe	44.7	47.0	4.7	1.2	–	34.0	50.0	15
Macronuclear nodule, length	aus	5.1	4.5	1.8	0.5	35.0	3.0	9.0	12
	eda[c]	4.0	4.0	0.0	–	–	4.0	4.0	10
	hal	12.1	15.0	4.0	–	–	6.0	17.0	17
	spe	18.6	20.0	3.1	0.8	–	11.0	23.0	15
Macronuclear nodule, width	aus	3.2	3.0	0.6	0.2	19.4	2.5	4.5	12
	hal	7.0	7.0	0.9	–	–	6.0	9.0	17
	spe	7.3	7.0	1.7	0.4	–	5.0	12.0	15
Macronuclear nodules, distance in between	spe	24.7	25.0	2.8	0.7	–	20.0	30.0	15
Macronuclear nodules, number	aus	18.4	15.5	5.4	1.6	29.3	13.0	28.0	12
	eda	16.8	16.0	1.5	–	–	15.0	20.0	10
	hal	9.6	10.0	2.0	–	–	5.0	14.0	17
	spe	2.0	2.0	0.0	0.0	–	2.0	2.0	15
Micronucleus, length	aus	2.7	–	–	–	–	2.5	3.8	3
	spe	2.0	2.0	0.0	0.0	0	–	–	5
Micronucleus, width	aus	1.9	.6	–	–	–	1.5	2.7	3
	spe	2.0	2.0	0.0	0.0	0	–	–	5
Micronuclei, number	aus	1.5	1.5	0.6	0.3	38.5	1.0	2.0	4
	eda	4.0	4.0	0.0	–	–	4.0	4.0	10
	hal	2.9	3.0	0.6	–	–	2.0	4.0	10
	spe	2.0	2.0	0.0	0.0	–	–	–	5
Adoral zone of membranelles, length	aus	32.1	33.5	5.2	1.5	16.3	22.0	39.0	12
	eda	38.4	39.0	2.8	–	–	32.0	41.0	10
	hal	54.5	55.0	4.4	–	–	44.0	60.0	17
	spe	50.5	52.0	4.6	1.2	–	45.0	57.0	15
Adoral membranelles, number	aus	24.3	25.0	2.5	0.7	10.1	20.0	27.0	12
	eda	21.3	21.0	.9	–	–	20.0	23.0	10
	hal	24.3	24.0	0.6	–	–	24.0	26.0	17
	spe	30.8	31.0	2.2	0.6	–	25.0	34.0	15
Frontal cirri, number	aus	3.0	3.0	0.0	0.0	0.0	3.0	3.0	9
	eda[d]	8.4	8.0	0.4	–	–	8.0	9.0	10
	hal[d]	9.0	9.0	0.7	–	–	8.0	10.0	16
	spe[d]	8.4	8.0	0.5	0.1	–	8.0	9.0	15
Buccal cirri, number	aus	3.3	3.0	1.0	0.3	29.7	1.0	5.0	12
Parabuccal cirri, number[b]	aus	4.3	4.0	1.1	0.3	24.6	3.0	7.0	10
Left frontoventral row, number of cirri	aus	18.3	17.5	7.4	2.1	40.4	8.0	33.0	12
	eda	18.2	16.0	3.5	–	–	14.0	22.0	10
	hal	18.7	9.0	2.8	–	–	11.0	23.0	17
	spe	16.9	16.0	2.2	0.5	–	14.0	20.0	15
Right frontoventral row, number of cirri	aus	18.3	18.0	3.7	1.1	20.1	14.0	26.0	12

Table 19 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Right frontoventral row, number of cirri	eda	7.9	7.0	1.9	–	–	6.0	11.0	10
	hal	28.5	28.0	1.4	–	–	27.0	31.0	17
	spe	5.0	5.0	0.0	0.0	–	–	–	15
Left marginal row, number of cirri	aus	22.3	22.0	4.6	1.4	20.6	14.0	33.0	11
	eda	19.4	19.0	1.4	–	–	18.0	23.0	10
	hal	21.6	21.0	2.3	–	–	19.0	26.0	17
	spe	18.2	18.0	2.1	0.5	–	15.0	22.0	15
Right marginal row, number of cirri	aus	26.2	25.5	5.0	1.4	19.1	20.0	39.0	12
	eda	25.4	26.0	3.1	–	–	20.0	30.0	10
	hal	29.5	30.0	1.8	–	–	26.0	34.0	17
	spe	23.3	23.0	2.4	0.6	–	20.0	27.0	15
Dorsal kineties, number	aus	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	eda	3.0	3.0	0.0	–	–	3.0	3.0	10
	hal	3.0	3.0	0.0	–	–	3.0	3.0	17
	spe	3.0	3.0	0.0	0.0	–	3.0	3.0	15
Caudal cirri, number	aus	2.3	3.0	1.2	0.5	51.9	0.0	3.0	6
	eda	3.0	3.0	0.0	–	–	3.0	3.0	10
	hal	3.0	3.0	0.0	–	–	3.0	3.0	17
	spe	3.0	3.0	0.0	0.0	–	–	–	15

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] Cirri behind right frontal cirrus, that is, frontal cirrus not included.

[c] Diameter is given.

[d] All cirri formed by anlagen I–III (frontal cirri, buccal cirri, parabuccal cirri) included. Note that the *C. halophila* specimen illustrated has only seven frontal cirri, indicating that the morphometry is not quite correct.

[e] The minimum value (5) and sample size (1) are like incorrect.

Dorsal bristles arranged in three kineties; kinety 1 distinctly, kinety 2 slightly, and kinety 3 not shortened anteriorly in specimen illustrated (Fig. 48l). One caudal cirrus at rear end of each kinety. Caudal cirri 15 µm long and thus distinctly projecting; length of dorsal bristles not mentioned.

Occurrence and ecology: *Cladotricha australis* is obviously confined to saline soils and perhaps endemic in Australia because so far not recorded from Africa and other biogeographic regions (Foissner 1998, p. 200; Foissner et al. 2002a). Type locality of *C. australis* is the bank of Lake Alexandrina (Point Pelican) near the city of Adelaide, Australia, where Blatterer & Foissner (1988; p. 4, "FO 15") discovered it with low abundance in the rhizosphere of a highly saline soil (pH 7.1; 0 m above sea level; collector W. Foissner, 11.02.1987) grown with halophytes and tufts of grass. The type locality of the synonym *C. edaphoni* is the Coorong National Park, a lagoon region created by tectonic shifts in the Pleistocene, between Adelaide and Kingston where Wilbert (1995) found numerous specimens in a soil sample from a

dried-out salt lake (pH 8.8; salinity 26–57‰). No further records published. Both type localities are very close together. Feeds on long bacteria and spores of fungi (Blatterer & Foissner 1988).

Cladotricha halophila Wilbert, 1995
(Fig. 49a–s, Table 19)

1984 ***Cladotricha* spec.** – Nießen, Diploma thesis, p. 58, Abb. 16a–k, Table on p. 58 (Fig. 49a–s; description of morphology and cell division; see nomenclature).

1995 ***Cladotricha halophila* sp. n.**[1] – Wilbert, Acta Protozool., 34: 276, Fig. 8a–c, 9a–f, i, k, Table 9 (Fig. 49a–s; original description; the type material is deposited in the Zoological Institute of the University of Bonn [Poppelsdorfer Schloß], Germany).

2001 ***Cladotricha halophila* Wilbert, 1995** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 15 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

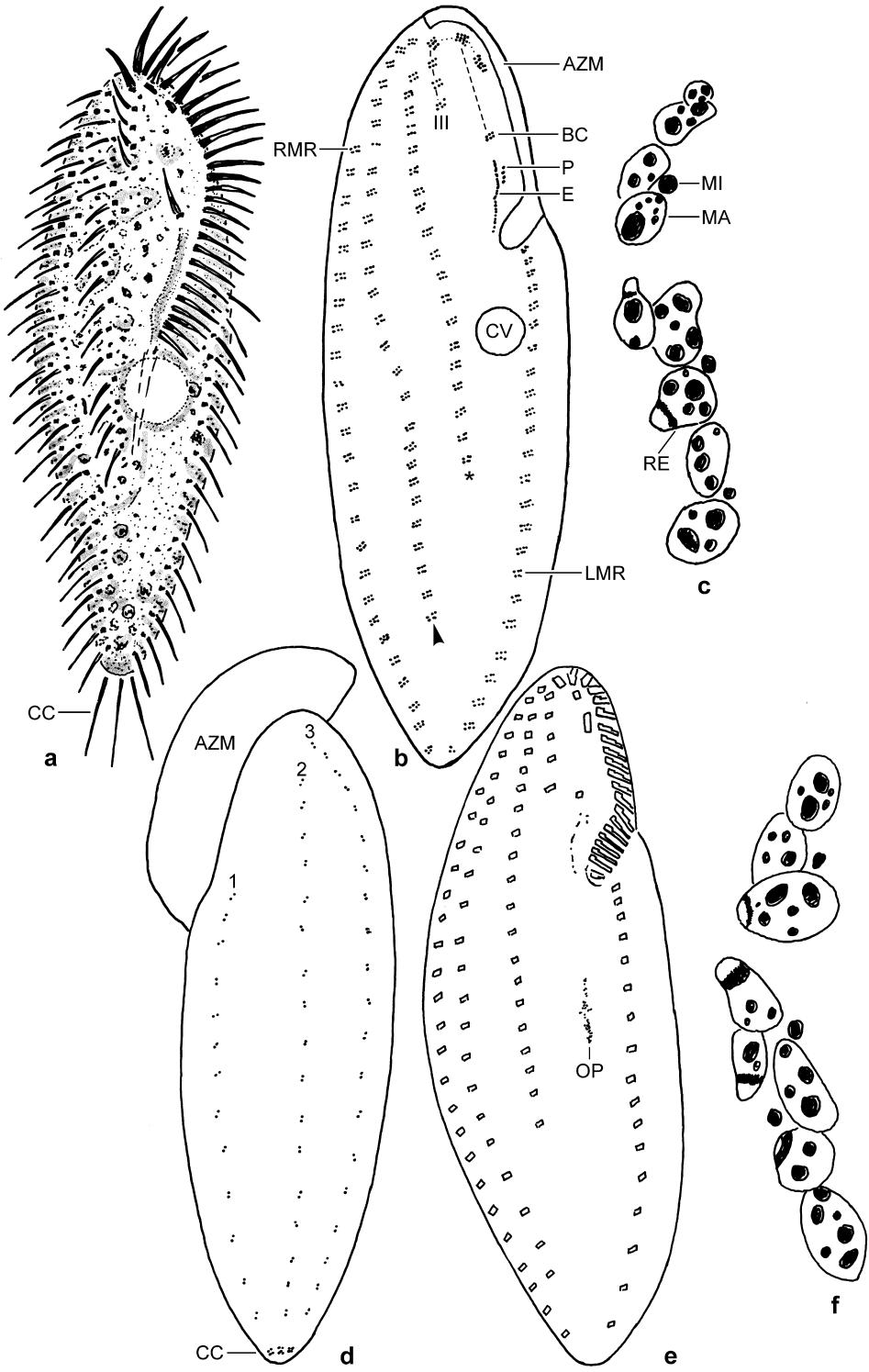
Nomenclature: No derivation of the species-group name is given in the original description. The name *halophil·us, -a, -um* (Latin adjective [m; f; n]; thriving in saline habitats) is a composite of the Greek words *halós* (salt) and *philos* (preferring), referring to the saline habitat where the species was discovered.

This species was first described, but not validly published (no species-group name assigned; thesis paper) by Nießen (1984). Eleven years later, Wilbert – who was very likely the supervisor of the thesis – provided the valid publication (Wilbert 1995). Since Nießen is not mentioned in the original description, Wilbert is deemed to be the author (ICZN 1999, Article 50.1.1).

Remarks: *Cladotricha halophila* closely resembles *C. australis*, so that synonymy cannot be excluded (further details see remarks at *C. australis*). According to Eigner (1997, p. 558), *C. halophila* is possibly the junior synonym of *Orthoamphisiella franzi*, now *Neowallackia franzi* (p. 281; see there for details). Eigner (1999,

Fig. 49a–f *Cladotricha halophila* (after Wilbert 1995. a, from life; b–f, protargol impregnation). The illustrations in the original description are so tiny that they could not be used; therefore sophisticated details (e.g., exact number and arrangement of basal bodies within cirri) in the redrawings must not be overinterpreted (for better illustrations, see Nießen 1984). **a:** Ventral view, about 170 µm. **b, c:** Infraciliature of ventral side and nuclear apparatus, about 115 µm. Asterisk marks rear end of left, arrowhead rear end of right frontoventral row. Dotted line connects frontal cirri. Broken lines connect cirri originating from same anlage (only shown for anlagen II and III). **d:** Infraciliature of dorsal side (same specimen as Fig. 49b, c?). **e, f:** Infraciliature of ventral side and nuclear apparatus of very early divider, about 105 µm. Details see text. AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri, CV = contractile vacuole, E = endoral, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, OP = oral primordium, P = paroral, RE = replication band, RMR = anterior end of right marginal row, III = frontoventral cirral row III (= right frontal cirrus and parabuccal cirri), 1–3 = dorsal kineties. Page 270. →

[1] Wilbert (1995) provided the following diagnosis: In vivo 102–172 × 25–39 µm, spindle-shaped *Cladotricha* with ca 10 macronuclear nodules, 3 caudal cirri, 2 ventral rows of cirri and 3 dorsal kineties. Frontal cirri conspicuously thickened.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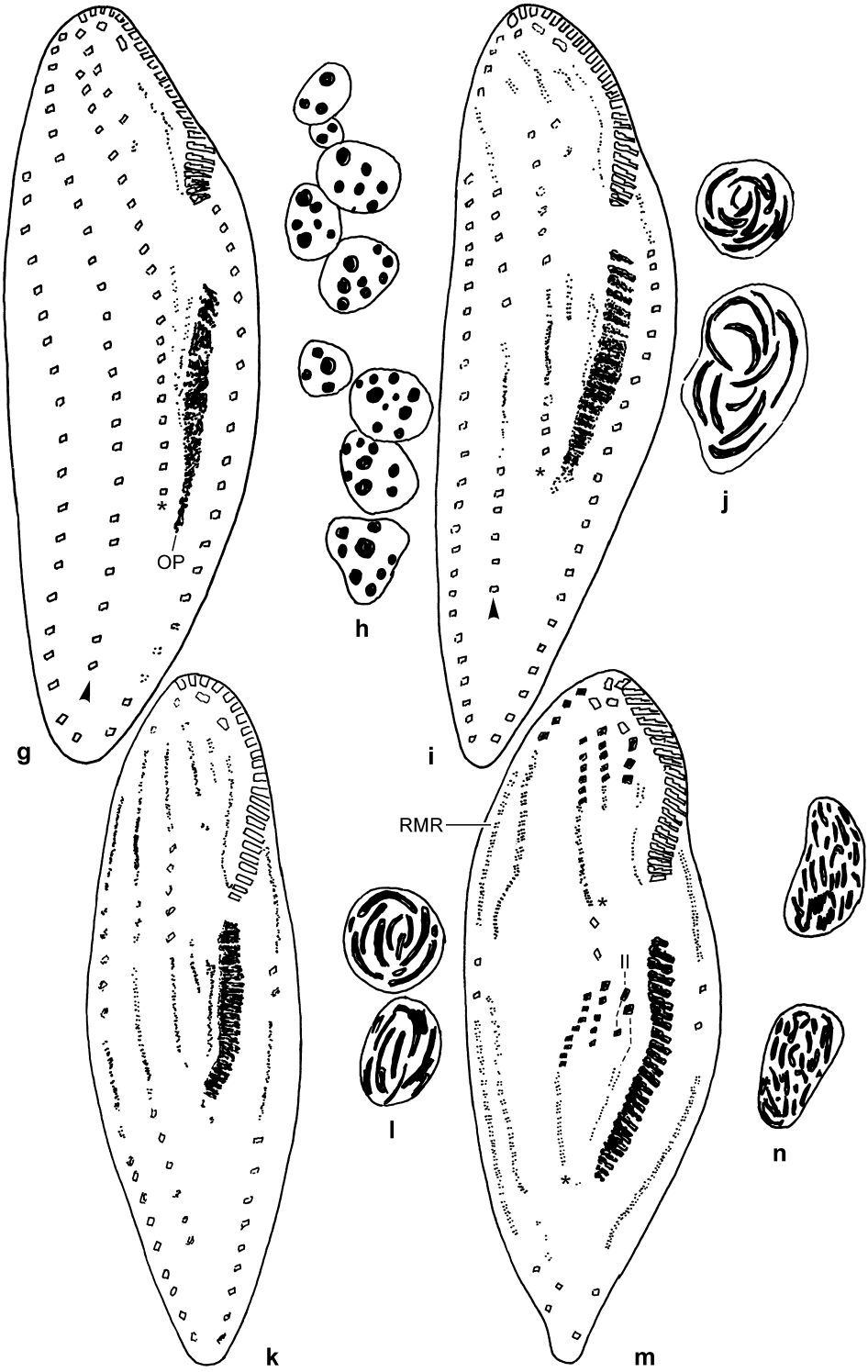
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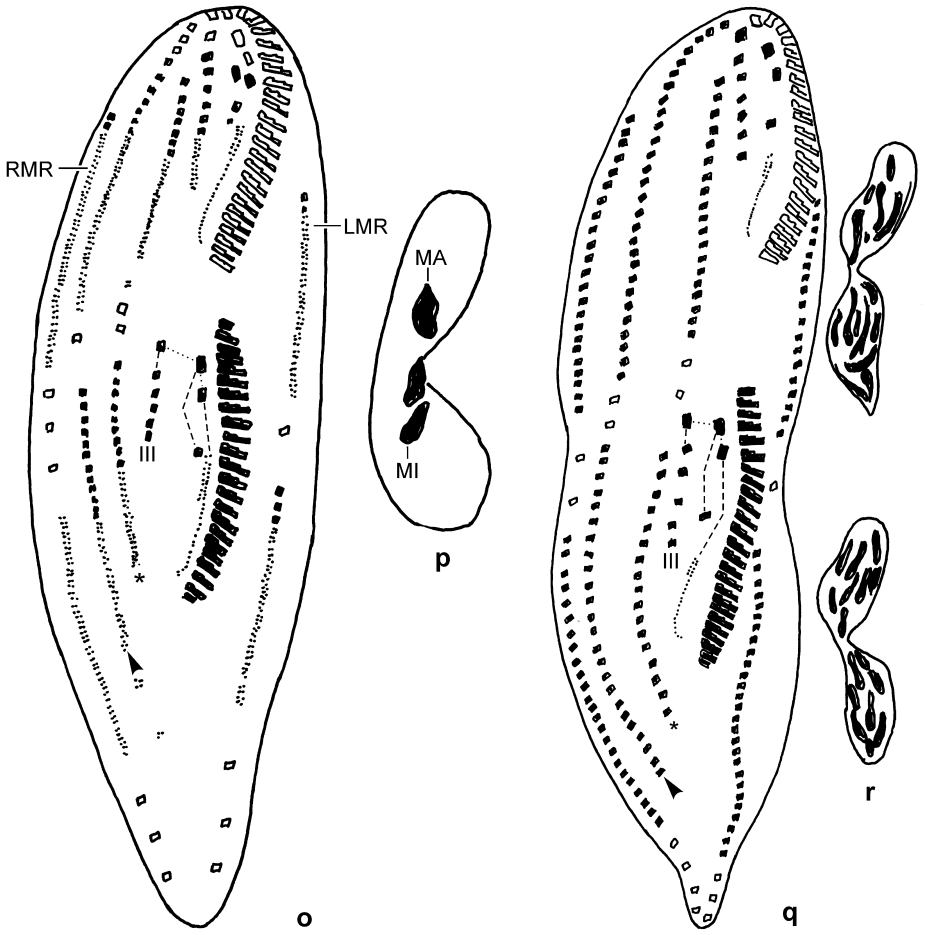

Fig. 49o–r *Cladotricha halophila* (after Wilbert 1995. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus of late (o, p, about 200 µm) and very late (q, r, about 200 µm) divider. The illustrations in the original description are so tiny that they could not be used; therefore sophisticated details (e.g., exact number and arrangement of basal bodies) in the redrawings must not be overinterpreted (for better illustrations, see Nießen 1984). Parental structures white, new black. Asterisk marks rear end of new left frontoventral row of opisthe, arrowhead denotes new right frontoventral row. Dotted line connects frontal cirri of opisthe, broken lines connect cirri originating from anlagen I–III. Details see text. LMR = new left marginal row of proter, MA = fused macronucleus, MI = micronucleus, RMR = new right marginal row of proter, III = new frontoventral row III of opisthe. Page 273.

← **Fig. 49g–n** *Cladotricha halophila* (after Wilbert 1995. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus of dividers. The illustrations in the original description are so tiny that they could not be used; therefore sophisticated details (e.g., exact number and arrangement of basal bodies) in the redrawings must not be overinterpreted (for better illustrations, see Nießen 1984). Asterisk marks rear end of left frontoventral row (g, i, parental; m, new), arrowhead denotes right frontoventral row (g, i). Details see text. **g, h:** Early divider, about 120 µm. **i, j:** Middle divider, about 180 µm. **k, l:** Middle to late divider, about 175 µm. **m, n:** Late divider, about 175 µm. Broken lines connect cirri/membranes originating from same anlage (only shown for anlagen I and II). OP = oral primordium, RMR = new right marginal row of proter, II = cirri anlage II. Page 270.

p. 46), who refrained from his own proposal, assigned it to the Orthoamphisiellidae because an anlage is formed in the rightmost frontoventral row.

Morphology: Body size 102–172 × 25–39 µm, length:width ratio of live specimen illustrated about 3:1 (Fig. 49a), 4.6:1 on average in protargol preparations (Table 19), indicating that the live specimen illustrated is markedly wide. Body outline fusiform, anterior end normal, posterior one narrowly rounded or inconspicuously pointed. Body particularly flexible and changeable (variable?) in the frontal region. On average 10 macronuclear nodules of variable shape and size and with varyingly large chromatin bodies arranged along midline; usually three micronuclei in between. Contractile vacuole more or less close behind buccal vertex, in specimen illustrated in Fig. 49a about at 50%, in specimen shown in Fig. 49b at 44% of body length. Presence/absence of cortical granules not mentioned. Cytoplasm light and colourless, with fine inclusions; posterior body portion often dark, evidently due to accumulation of (assembling) defecation vacuoles. Presence/absence of cortical granules not mentioned. Slowly rotating about main body axis or jerky swaying.

Oral apparatus gonostomatid, occupies about 39% of body length and composed of 24 membranelles on average (Fig. 49a, b, Table 19). Paroral left of anterior end of endoral, composed of four basal bodies/cilia in specimen illustrated; endoral curved, extends to buccal vertex (note that Wilbert confused endoral and paroral; see *C. edaphoni* above).

Cirral pattern as shown in Fig. 49b and therefore very similar as in *C. australis*. Frontal cirri rather thick (composed of three rows of basal bodies) and arranged in *Gonostomum*-pattern, that is, left cirrus distinctly displaced posteriad. Almost invariably one buccal cirrus[1] somewhat ahead of undulating membranes, perhaps a further difference to *C. australis* where the rearmost one is right of the anterior end of the membranes. Parabuccal row extends to about level of buccal cirrus. Left frontoventral row slightly shortened anteriorly, extends to about 60% of body length in specimen illustrated, right frontoventral row, which commences close to distal end of adoral zone, to 78% of body length (Fig. 49b). Right marginal row distinctly shortened anteriorly, that is, commences about at 22% of body length, terminates at rear end and therefore only indistinctly separated from rear end of left marginal row, which begins close to buccal vertex.

Dorsal bristles about 4 µm long, arranged in three kineties; left one (= kinety 1) distinctly, middle one slightly shortened anteriorly. Each kinety with one about 12 µm long caudal cirrus (Fig. 49d).

Cell division (Fig. 49e–s): This part of the life cycle is described with seven stages by Nießen (1984) and Wilbert (1995). Unfortunately, the illustrations in Wilbert (1995) are so tiny that many details are almost not recognisable.

Stomatogenesis: This part of cell division commences with the de novo formation of an oral primordium in the postoral area between the left marginal row and the left frontoventral row (Fig. 49e). Subsequently, the oral primordium becomes larger

[1] In only one specimen illustrated (proter in Fig. 49o) two buccal cirri are formed (perhaps the small one is resorbed during/after division).

and the formation of new membranelles begins anteriorly. Two anlagen have formed right of the oral primordium. The parental buccal cirrus and the undulating membranes have modified to primordia (Fig. 49g). Somewhat later the formation of membranelles continues and anlage I becomes more distinct (Fig. 49i, k). The left frontal cirrus originates very likely as is usual, that is, from the anterior end of anlage I. The parental adoral zone is retained for the proter (Fig. 49m, o, q).

Frontal-ventral cirri: In the proter the anlagen for the frontal-ventral cirri originate from the parental structures (Fig. 49g, i, k): anlage I, that is, the left frontal cirrus originates from the undulating membrane anlage; anlage II from the modified buccal cirrus; anlage III obviously from one or two parabuccal cirri; left frontoventral row originates from anteriormost cirrus/cirri of parental left frontoventral row; and right frontoventral row from parental cirri in the anterior portion of the right row. In the opisthe, the situation is not quite clear. The left frontal cirrus originates from the undulating membrane anlage; the origin of anlagen II and III is uncertain, but probably they are formed from the oral primordium, as is usual for most hypotrichs; the anlagen for the left and right frontoventral row originate within the parental rows (Fig. 49i, k).

Marginal cirri and dorsal infraciliature (Fig. 49d, s): The anlagen of the marginal row occur within the parental rows. Dorsal morphogenesis proceeds in *Gonostomum*-pattern, that is, within the parental rows 1–3 each two anlagen are formed, one for the proter and one for the opisthe. At the end of each kinety a caudal cirrus originates. Dorsomarginal kineties and kinety fragmentation are lacking.

Nuclear apparatus (Fig. 49f, h, j, l, n, p, r): Replication bands occur before the oral primordium is formed (Fig. 49c). Later, the macronuclear nodules fuse successively to a single mass, which later divides into the species-specific number of nodules.

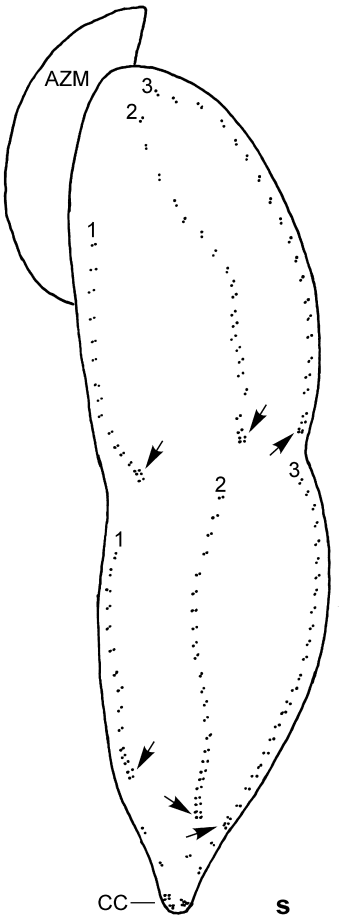

Fig. 49s *Cladotricha halophila* (after Wilbert 1995. Protargol impregnation). Infraciliature of dorsal side of very late divider, body length about 220 µm. Arrows mark new caudal cirri. AZM = adoral zone of membranelles, CC = parental caudal cirri, 1–3 = new dorsal kineties. Page 270.

Occurrence and ecology: Likely confined to saline habitats. The type locality of *C. halophila* is very close to that of *C. australis* and probably identical with that of its synonym *C. edaphoni*, that is, the Coorong National Park, a lagoon region created

by tectonic shifts in the Pleistocene, between Adelaide and Kingston. Wilbert (1995) found numerous specimens in a soil sample from a dried out salt lake (pH 8.1–9.5; salinity 24–66‰). Feeds likely on bacteria (Nießen 1984, Wilbert 1995). Good culturable. Shortly before a culture perished many specimens were atypical as concerns body shape and movement. The specimens were conspicuously slender and had a tail (Nießen 1984).

Incertae sedis in *Cladotricha*

Strongylidium packii (Calkins in Pack, 1919) Kahl, 1932
(Fig. 50a–e)

1919 ***Uroleptus packii* Calkins** – Pack, Biol. Bull. mar. biol. Lab. (Woods Hole), 36: 277, Fig. 1, 2 (Fig. 50a, b; original description; no formal diagnosis provided and no type material available).

1932 ***Strongylidium (Uroleptus) packi* Calkins, 1919** – Kahl, Tierwelt Dtl., 25: 554, Fig. 86 $_{23, 24}$ (Fig. 50c, d; combination with *Strongylidium*; review; incorrect subsequent spelling).

1933 ***Strongylidium packi* (Calkins 1919)** – Kahl, Tierwelt N.- u. Ostsee, 23: 105, Fig. 16.2 (Fig. 50e; guide to marine ciliates; incorrect subsequent spelling).

1972 ***Strongylidium packi* Calkins in Pack, 1919** – Borror, J. Protozool., 19: 13 (revision of hypotrichs; incorrect subsequent spelling and incorrect presentation of author and date).

2001 ***Uroleptus packii* Calkins in Pack, 1919** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 98 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs; see nomenclature).

2007 ***Strongylidium packi* (Calkins in Pack, 1919)** – Paiva & Silva-Neto, Zootaxa, 1559: 52, Fig. 12c–f (Fig. 50a–d; brief revision of *Strongylidium*; incorrect subsequent spelling).

Nomenclature: Gary N. Calkins has checked this form and, provisionally, named it *Uroleptus packii*, obviously to honour the collector of the sample and author of the paper (Pack 1919, footnote on p. 277); this designation was taken over by Pack (1919). In the catalogue of ciliate names I incorrectly assumed that Jankowski (1979) has transferred this species from *Uroleptus* to *Strongylidium* (Berger 2001). The spelling in Kahl (1932) does not mean that he considered *Uroleptus* as subgenus of *Strongylidium*, but should simply indicate that this species was originally classified in *Uroleptus*.

Remarks: The list above comprises the original description of this Great Salt Lake hypotrich and some well known papers. According to the reviews by Stephens (1974) and Hammer (1986), this species was recorded by some other workers from the same locality when they made their dissertations.

Pack (1919) made no comment why he and Calkins, respectively, have assigned this species to *Uroleptus* – a genus which was already well defined via the two narrowly spaced ventral rows at that time (see Stein 1859, Bütschli 1889) – although the present species has only one ventral row. Kahl (1932) recognised the misclassification in *Uroleptus* and transferred it without explanation to *Strongylidium*, obviously because of the spiralled cirral rows. Kahl's generic assignment was taken over by Borror (1972), who considered it, again following Kahl (1932), as senior synonym

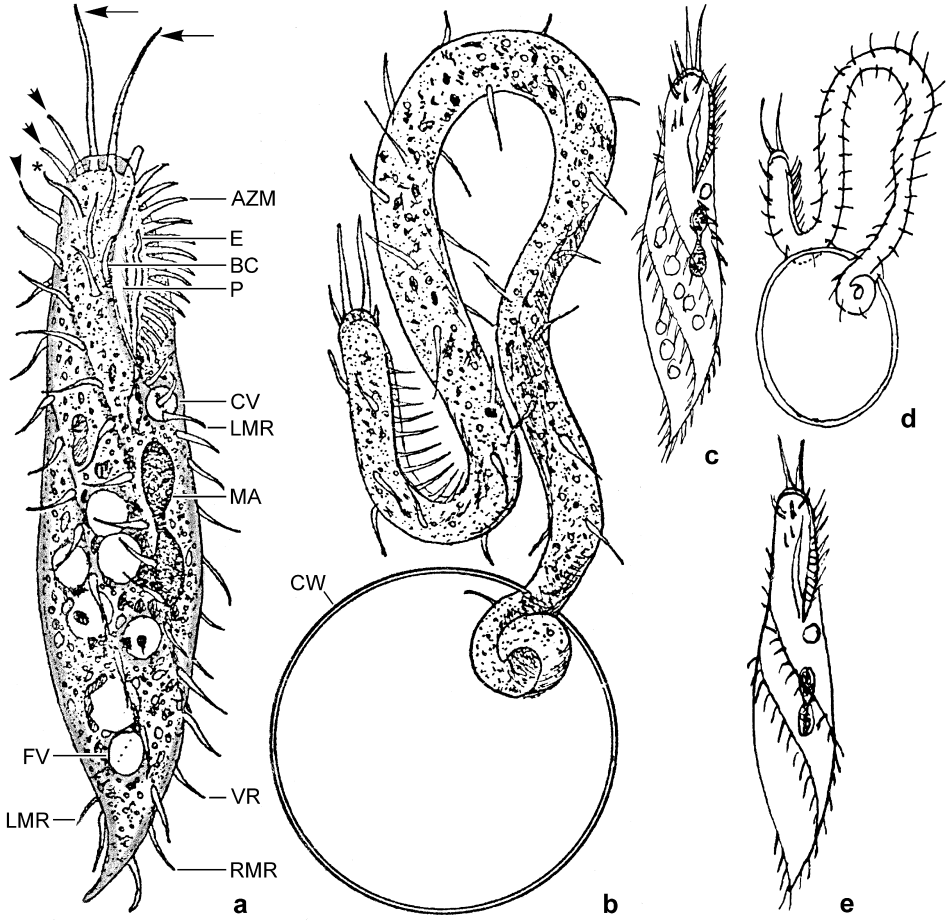

Fig. 50a–e *Strongylidium packii* (a, b, from Pack 1919; c, d, after Pack 1919 from Kahl 1932; e, after Pack 1919 from Kahl 1933. From life). **a, c, e:** Ventral view, specific size not indicated (about 70 µm). Long arrows mark the two anteriormost adoral membranelles, termed feeling cirri by Pack (1919); short arrows obviously mark the last and the penultimate adoral membranelles, termed frontal cirri by Pack (1919); asterisk marks the right frontal cirrus (see text); arrowhead denotes anterior end of frontoventral row. **b, d:** Excysting specimens are long and slender. AZM = adoral zone of membranelles, BC = buccal cirrus, CV = contractile vacuole, CW = cyst wall, E = tongue-shaped endoral?, FV = food vacuole, LMR = left marginal row, MA = dumbbell-shaped macronucleus, P = paroral, RMR = right marginal row, VR = frontoventral row. Page 276.

of *Cladotricha koltzowii*. With this approach, Borror (1972) submerged *Cladotricha* in *Strongylidium* (see genus section).

Hemberger (1982) listed Pack (1919) in the reference section, but I did not find *U. packii* in the text, neither as valid species nor as synonym. Since main features of *U. packii* are not known (e.g., details of oral apparatus, exact cirral pattern, dorsal infraciliature), I preliminary accept Kahl's classification in *Strongylidium*, but re-

view it under *Cladotricha* because it is halophilous. Perhaps *S. packii* is endemic in the Great Salt Lake, although the lake is not very old, that is, 12.000 to 30.000 years (Flowers & Evans 1966, p. 368).

I found no distinct difference between *Strongylidium packii* and *Cladotricha sigmoidea* (Fig. 45a), except for the symbiotic algae which "probably" cause the pale green colour of *S. packii* (Pack 1919, p. 279). Thus, I preliminary refrain from a synonymy and suggest to study further populations from the faraway type localities, a salt lake in southern Australia and the Great Salt Lake in the USA.

Vorhies (1917, p. 497) found few specimens closely resembling a species of *Uroleptus* in Great Salt Lake, perhaps the first record of the present species.

Morphology: Body length about 70 µm at a salinity of 230‰; length:width ratio of specimen illustrated 4.5:1 (Fig. 50a). Body roughly spindle-shaped with anterior end rounded and posterior end tapered; quite rigid, that is, keeping characteristic body shape. Body pale green coloured, probably due to symbiotic algae according to Pack (1919). Macronucleus dumbbell-shaped, that is, obviously composed of two ellipsoidal nodules connected by a rather thick isthmus; micronucleus not described. Contractile vacuole close behind proximal end of adoral zone. Presence/absence of cortical granules not mentioned. Up to 30 food vacuoles present. Cytopyge on dorsal side in rear body portion. According to Pack (1919), *Strongylidium packii* is a very active form with a creeping or swimming forward movement of 100 µm per 7 s and a darting backward movement of double this speed; according to the table on page 275 in Pack (1919), this speed refers to a medium density of about 1.1, that is, distinctly below the density of 1.2 at a salinity of 230‰. The backward movement generally follows irritation at the anterior end.

Adoral zone according to illustration without peculiarities, that is, not clearly gonostomatid; occupies about 25% of body length in specimen illustrated (Fig. 50a). Anteriormost two membranelles 17–20 µm long at a salinity of 230‰, about twice as long as other membranelles (Fig. 50a). Paroral obviously rather prominent, indicating that it is not as short and composed of few, widely spaced cilia as in some other well described *Cladotricha* species. Pack (1919) described, but did not label a second, tongue-like undulating membrane "along the floor of the peristomial region" (actually this is obviously the endoral on the roof of the buccal cavity). Cytopharynx a "swollen tube" extending from the cytostome dorsally.

Cirral pattern not known in all details. Specimen illustrated with two transversely arranged (frontal?) cirri somewhat behind frontal scutum; one buccal cirrus right of anterior half of paroral; and two cirri behind right "frontal" cirrus. Frontoventral row commences near distal end of adoral zone, extends spirally to near rear cell end. Anteriormost right marginal cirrus illustrated about at level of buccal cirrus, right row extends parallel to frontoventral row and terminates slightly subcaudally. Left marginal row commences at proximal end of adoral zone, spirally arranged and ending subterminally like other two rows.

Dorsal infraciliature (number and arrangement of dorsal kineties; length of bristles; presence/absence of caudal cirri) not described.

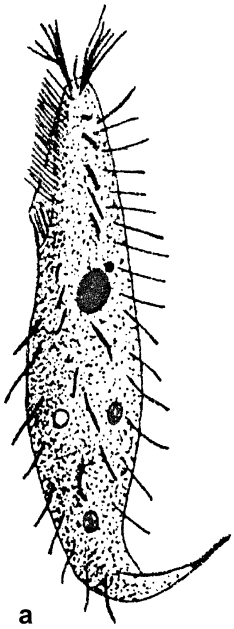

Fig. 51a Insufficient redescription of *Cladotricha koltzowii* (from Madrazo-Garibay & López-Ochoterena 1973. From life?). Ventral infraciliature seen from dorsal, 180 µm. The illustration closely resembles Fig. 43a, indicating that it is a redrawing. Page 280.

Cell division, conjugation, cyst (Fig. 50b): Pack (1919) observed transverse and "longitudinal" fission[1], and conjugation is followed by rapid division. At certain times, perhaps after a full meal, *S. packii* encysts and may remain in this stage for 50 d. When it becomes active again, it breaks through the cyst wall as a much elongated form (Fig. 50b). After swimming for a short period in this form it divides transversely and rounds up into a cyst if the opisthe is not sufficiently organised.

Occurrence and ecology: *Strongylidium packii* is very likely confined to highly saline habitats. Type locality is the south-eastern shore of Great Salt Lake (salinity 230‰) in the vicinity of the Salt Air Pavilion, about 25 km west of Salt Lake City, Utah, USA. Pack (1919) collected the material on 30. April 1918. The lake itself is about 12.000 to 30.000 years old (Flowers & Evans 1966, p. 368), that is, it cannot be excluded that *Strongylidium packii* is endemic in the Great Salt Lake.

According to Hammer (1986, p. 371), Jones (1945) recorded the present species from the Great Salt Lake at a salinity from about 165–265‰.[2] It is also listed in some reviews on the Great Salt Lake (e.g., Flowers & Evans 1966, p. 374; Stephens 1974, p. 225). According to Stephens (1974, p. 223), Kirkpatrick (1934) also found *U. packii* in this lake.

Pack (1919) studied the effect of dilution on various factors. When the density of the medium was 1.2, *Strongylidium packii* needed 10 min for a distance of 100 µm; at a density of 1.11 the time was 7.5 s, at 1.06 only 1–2 s. At densities below 1.03 the anteriormost frontal membranelles moved hundreds times faster than at a density of 1.22 when one stroke of these membranelles occupied 5 s; in the density of 1.11 the membranelles made about five strokes per second. In addition, the length of the frontal membranelles depended on the density of the medium (17–20 µm at saturation; 10–11 µm at 1.03). When kept in saturated solution, *S. packii* is sensitive to light (Pack 1919). *Strongylidium packii* feeds on bacteria, small plants and animals which abound in the water (Pack 1919).

[1] Perhaps this is another term for conjugation, which was also observed.

[2] Since I do not have the paper by Jones (1945), I do not know whether the data are original or those from Pack (1919).

Insufficient redescription

***Cladotricha koltzowii* Gajevskaja, 1925** – Madrazo-Garibay & López-Ochoterena, 1973, Revta Soc. mex. Hist. nat., 34: 66, Fig. 8 (Fig. 51a). Remarks: This population is from the Salto de San Anton, a large ravine with a small waterfall located within the city limits of Cuernavaca, State of Morales, Mexico (see also Madrazo-Garibay & López-Ochoterena 1982, p. 292). Neither the associated ciliate cenosis nor other information indicates that this is a saline water. Thus, it is extremely unlikely that the identification is correct, even if the specimen illustrated almost perfectly matches Fig. 50a of the original description. I suppose that this is not an original observation, but a slightly modified or rough redrawing of Fig. 50a. Thus, the brief recapitulation of the Mexican description contains only data deviating from the original description. An acceptance of the identification would destroy the ecology of *C. koltzowii* as an inhabitant of highly saline habitats. Probably it will never be possible to identify the specimens observed by the Mexican workers; perhaps it was an uroleptid. Body size 180 × 37 µm; contractile vacuole in posterior body third.

Neowallackia gen. nov.

Nomenclature: *Neowallackia* is a composite of the Greek adjective *néos* (new, young, fresh) and the genus-group name *Wallackia* (see p. 206 for derivation). It insinuates the possibility that it is closely related to *Wallackia*. Like *Wallackia* feminine gender.

Characterisation (A = supposed apomorphy): Oral apparatus gonostomatid. Frontal-ventral cirri formed from five anlagen only (A?). Anlagen II–V[1] form more frontal-ventral cirri than that in 18-cirri hypotrichs. Transverse cirri lacking. One right and one left marginal row. Three bipolar dorsal kineties, that is, dorsomarginal kineties and dorsal kinety fragmentation lacking. Caudal cirri lacking (A). Terrestrial.

Type species: *Gonostomum franzi* Foissner, 1982.

Additional characters: Contractile vacuole close to proximal end of adoral zone of membranelles; cortical granules lacking (*N. franzi*), present (*N. ghangriai*), or presence/absence not described (*N. petergofi*).

Remarks: See type species.

Species included in *Neowallackia* (alphabetically arranged basionyms are given): (1) *Gonostomum franzi* Foissner, 1982 (type species); (2) *Paragonostomum ghangriai* Kamra, Kumar & Sapra, 2008; (3) *Trachelochaeta petergofi* Alekperov, 2005 (= *T. petergoffii*).

[1] I do not know which of the ordinary six (I–VI) frontal-ventral cirri anlagen is lacking. For the sake of simplicity the five anlagen are designated as I–V (details see remarks).

Key to *Neowallackia* species and similar species

When you know that your specimen/population belongs to *Neowallackia*, then species identification is simple and needs only live observation. If you cannot identify your specimen/population with the key below, see also *Wallackia* (p. 206), *Gonostomum* (p. 58), *Paragonostomum* (p. 172), *Cladotricha* (p. 235), or *Kahliella* (p. 347).

1 Two macronuclear nodules (Fig. 55a, b). **3**
- About 7–21, on average about 11 or 18 macronuclear nodules (Fig. 52a, e, 53b, 54a–c). **2**

2 Cortical granules and extrusomes lacking (Fig. 52a–f, 53a, b). . . . . *Neowallackia franzi* (p. 281)
- Cortical granules colourless, scattered; extrusomes present, stain with protargol (Fig. 54a–c). . . . . *Neowallackia ghangriai* (p. 295)

3 (1) Caudal cirri lacking (Fig. 55a, b). . . . . *Neowallackia petergofi* (p. 298)
- Caudal cirri prominent because long and shaped like a Pasteur-pipette (Fig. 40a–e). . . . . *Wallackia bujoreani* (p. 212)

Neowallackia franzi (Foissner, 1982) comb. nov.
(Fig. 52a–f, 53a–w, Table 20)

1982 ***Gonostomum franzi* nov. spec.**[1] – Foissner, Arch. Protistenk., 126: 74, Fig. 17a–e, 60, Tabelle 16 (Fig. 52a–f; original description; for type material, see nomenclature).

1988 ***Kahliella franzi* (Foissner, 1982) nov. comb.** – Berger & Foissner, Arch. Protistenk., 136: 65, 66, Fig. 3–25 (Fig. 53a–w; description of cell division and combination with *Kahliella*).

1995 ***Orthoamphisiella franzi* (Foissner, 1982) nov. comb.** – Eigner, Europ. J. Protistol., 31: 363 (combination with *Orthoamphisiella*).

1997 ***Orthoamphisiella franzi* (Foissner, 1982) Eigner, 1995** – Eigner, J. Euk. Microbiol., 44: 556, Fig. 6 (Fig. 53a; schematic presentation of cell division).

1999 ***Kahliella franzi* (Foissner, 1982) Berger & Foissner, 1988** – Berger, Monographiae biol., 78: 369 (brief note on the exclusion from the oxytrichids).

2001 ***Kahliella franzi* (Foissner, 1982) Berger and Foissner, 1988** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 29 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2008 ***franzi Gonostomum* Foissner, 1982** – Aescht, Denisia, 23: 156 (comments on deposition of type material; see nomenclature).

Nomenclature: Foissner (1982) dedicated this species to Herbert Franz[2], an Austrian soil biologist. "*Urostyla franzi* Foissner", provisionally published by Foissner

[1] Foissner (1982) provided the following diagnosis: In vivo etwa 100–130 × 28–40 µm großes, lang ovales, etwa 2–3:1 abgeflachtes *Gonostomum* mit je einer rechten und linken Marginalreihe und 4 zum Teil stark verkürzten, leicht schräg verlaufenden Ventralreihen. Durchschnittlich 12 kugelförmige bis ellipsoide Makronucleus-Teile. 3 Dorsalkineten.

[2] Both names are common first names in Austria, but in the present case Franz is the surname.

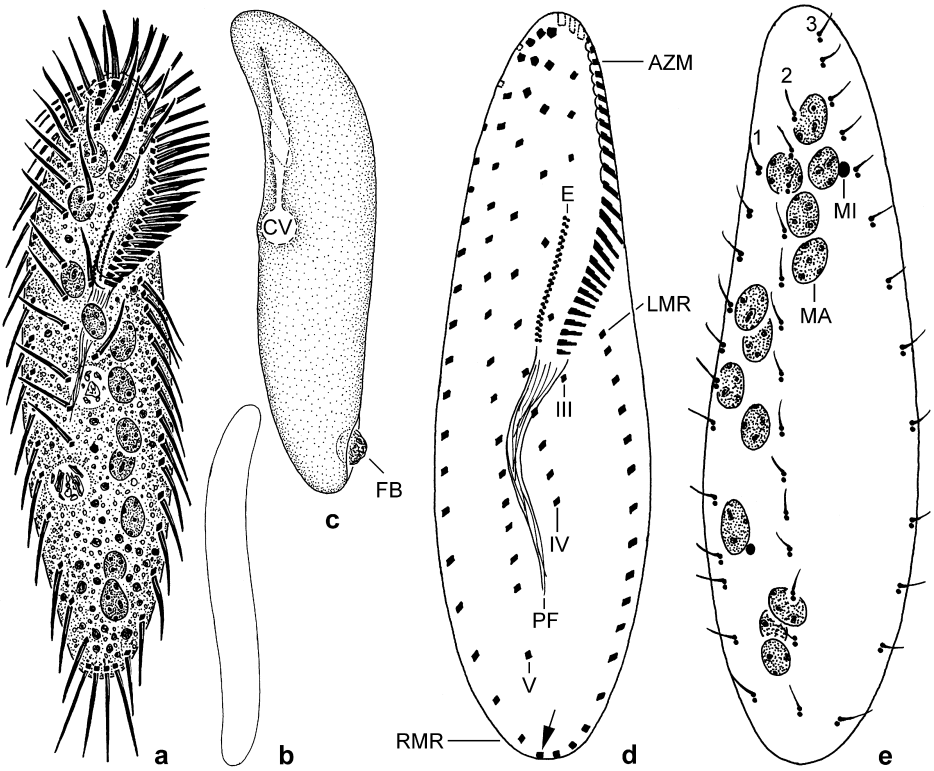

Fig. 52a–e *Neowallackia franzi* (from Foissner 1982. a–c, from life; d, e, protargol impregnation). **a:** Ventral view of a representative specimen, 123 µm. **b:** Lateral view, 128 µm. **c:** Dorsal view showing contractile vacuole with anteriorly extending collecting canal and defecation, 128 µm. **d, e:** Infraciliature of ventral and dorsal side and nuclear apparatus of same(?) specimen, 69 µm. Arrow in (d) marks rear end of left marginal row; the rearmost cirri of this row must not be misinterpreted as caudal cirri. AZM = adoral zone of membranelles, CV = contractile vacuole, E = endoral (paroral not illustrated), FB = faecal ball, LMR = anterior end of left marginal row, MA = macronuclear nodule, MI = micronucleus, PF = pharyngeal fibres, RMR = rear end of right marginal row, III–V = frontoventral rows, 1–3 = dorsal kineties. Page 281.

(1981, p. 19), is a nomen nudum and thus not available (ICZN 1999, Article 13 and Glossary). *Kahliella franzi* is not a basionym of *G. franzi*, as supposed by Eigner (1997, p. 556, legend), but a combination made by Berger & Foissner (1988). In addition, Eigner (1997, p. 558) erroneously mentioned *Kahliella franzi* as basionym of *Pseudokahliella marina* (see p. 663). Type species of *Neowallackia*. Incorrect subsequent spelling: *Gonostomum fransi* (Alekperov 2005, p. 219).

There exists rather great confusion about the deposition of the type material in this species. Foissner (1982) made not comments about this topic. According to Aescht (2003, p. 386), Foissner deposited one paratype slide (accession number 1982/79 according to Aescht 2003) from the type locality[1] (Guttal, Salzburg) in the

[1] I know that a paratype can come, per definition, only from the type material/series. However, in the pre-

Upper Austrian Museum in Linz (LI). Aescht (2008, p. 156) explained the situation more detailed. She wrote that three slides have been deposited by Foissner; one from the type locality is ambiguously labelled as "paratype" (interestingly, in Aescht 2008 the paratype slide has the accession number 1982/18[1] and not 1982/79 as indicated in her paper from 2003 [see above]). Since no specimen is marked on this slide, Aescht considered this slide as syntype. In addition, Foissner has deposited two further slides (accession numbers 1981/10, 1984/6), labelled as "holotype" and "paratype", although they are not from the type population from Guttal in Salzburg (see occurrence), but from the population studied by Berger & Foissner (1988) from the Lunz-area in Lower Austria (Aescht 2008, p. 156). Consequently, the slides from the Lunz-population are vouchers. The problem with the true type material is much more complex and therefore needs a detailed, separate analysis.

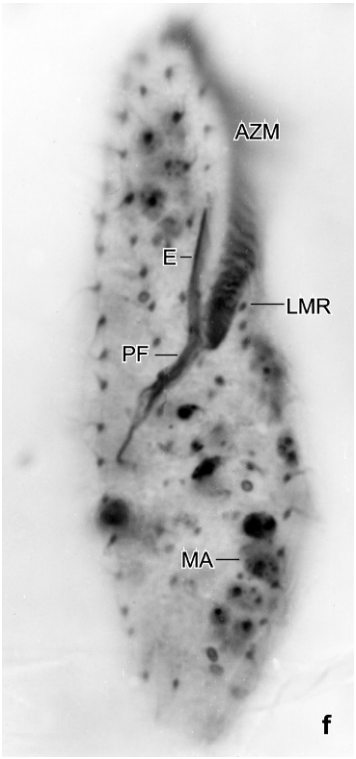

Fig. 52f *Neowallackia franzi* (from Foissner 1982. Protargol impregnation). Infraciliature of ventral side. AZM = adoral zone of membranelles, E = endoral, LMR = anterior end of left marginal row, MA = macronuclear nodule, PF = pharyngeal fibres. Page 281.

Remarks: As already mentioned by Foissner (1982), the generic assignment of the present species is rather uncertain. For each proposal made so far (*Gonostomum*, *Kahliella*, *Orthoamphisiella*) pros and cons exist. Originally it was assigned to *Gonostomum* because the general organisation (body shape) and the oral apparatus (short paroral; arrangement of endoral and paroral; gonostomatid shape of adoral zone) and some features of the somatic infraciliature (e.g., three dorsal kineties) are reminiscent on this genus, but also on *Wallackia* Foissner, 1976 and *Trachelochaeta* Šrámek-Hušek, 1954 (Foissner 1982). The problem is that transverse and caudal cirri are present in *Gonostomum*, whereas both cirral groups are lacking in *G. franzi*. However, transverse cirri are occasionally also absent in some specimens of *G. affine*, type of *Gonostomum* Sterki, 1878 (for review, see Berger 1999, p. 367 and present book, p. 68), and for that reason Foissner (1982) assigned it preliminary to *Gonostomum*. The major problem is that *Gonostomum* species have (inconspicuous) cortical granules (vs.

sent case the situation is rather tricky so that this has to be emphasised.

[1] Aescht (2008, p. 156) wrote "PP? (sd): 1982/18." (PP = paraphoront/"paratype", sd = subsequent designation). I do not know exactly what the term "subsequent designation" means in the present case; perhaps this refers to the fact that Aescht designated the paratype subsequently as syntype.

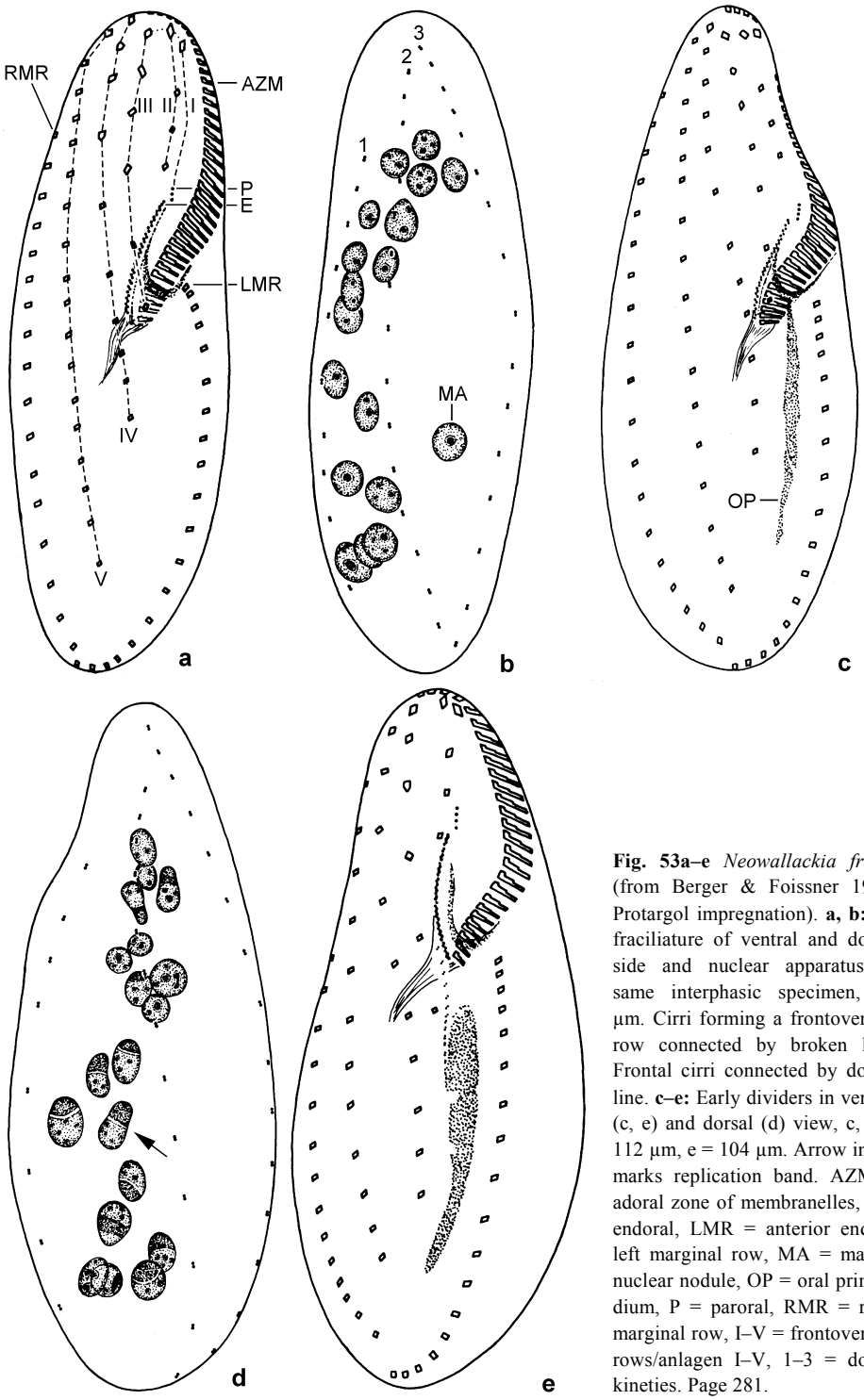

Fig. 53a–e *Neowallackia franzi* (from Berger & Foissner 1988. Protargol impregnation). **a, b:** Infraciliature of ventral and dorsal side and nuclear apparatus of same interphasic specimen, 98 µm. Cirri forming a frontoventral row connected by broken line. Frontal cirri connected by dotted line. **c–e:** Early dividers in ventral (c, e) and dorsal (d) view, c, d = 112 µm, e = 104 µm. Arrow in (d) marks replication band. AZM = adoral zone of membranelles, E = endoral, LMR = anterior end of left marginal row, MA = macronuclear nodule, OP = oral primordium, P = paroral, RMR = right marginal row, I–V = frontoventral rows/anlagen I–V, 1–3 = dorsal kineties. Page 281.

lacking in present species), their ventral ciliature originates from six frontal-ventral-transverse cirri anlagen (vs. five frontal-ventral cirri anlagen), and *G. affine* and *G. kuehnelti* have a cirral pattern closely resembling that of 18-cirri hypotrichs, whereas the cirral pattern of the present species reminded most authors to that of *Kahliella* or *Orthoamphisiella* (e.g., Hemberger 1982, Berger 1999, Eigner 1999, Foissner et al. 2002).

Maeda & Carey (1984, p. 4) excluded *G. franzi* from *Gonostomum* because it has ventral rows, but they did not propose another generic assignment. Berger & Foissner (1988) studied the cell division and could prove that transverse and caudal cirri are actually lacking, whereas both cirral groups are present in *Gonostomum*. Basically for that reason – and because *G. franzi*, *Kahliella acrobates*, and *K. simplex* have a similar cirral pattern – we transferred it to *Kahliella*. In addition, *Kahliella* species and the present species have a gonostomatid oral apparatus. However, there are also features contradicting a classification of the present species in *Kahliella*, for example, the lack of a dorsomarginal row (vs. present at least in *K. simplex*), the different number of frontal-ventral-cirral anlagen (five in present species vs. six in *K. simplex*), and the lack of parental cirral rows in postdividers (vs. present in *Kahliella*). Consequently, the classification in *Kahliella* is doubtful.

Indeed, Eigner (1995) considered the classification of *G. franzi* in *Kahliella* as incorrect because it shows none of the typical *Kahliella* features. He transferred it to *Orthoamphisiella* Eigner & Foissner, 1991 because the rightmost frontoventral row of *G. franzi* and *O. stramenticola* (type of *Orthoamphisiella*) is formed in the same way (Eigner & Foissner 1993). In addition, *Orthoamphisiella* species have lost, like *Kahliella*, transverse and (the ordinary) caudal cirri and they also lack, like the present species, parental cirral rows. However, a more detailed inspection shows that *Gonostomum franzi* differs from *O. stramenticola* in the following features: (i) shape of adoral zone of membranelles (gonostomatid vs. normal, that is, shaped like a question mark); (ii) shape of paroral (gonostomatid, that is, short because composed of only few cilia vs. roughly of ordinary length); (iii) number of dorsal kineties (three vs. two); (iv) the parental rightmost frontoventral row produces two independent anlagen (one for the proter, one for the opisthe) in *G. franzi*, whereas in *O. stramenticola* a single anlage (primary primordium) is formed, which splits somewhat later. In addition, many specimens of *O. stramenticola* have the ordinary number of six (I–VI) frontal-ventral cirri anlagen whereas constantly five anlagen are present in *G. franzi*. All these differences indicate that *G. franzi* should not be classified in *Orthoamphisiella*.

Cladotricha halophila Wilbert, 1995 is, according to Eigner (1997, p. 558), possibly a synonym of *Neowallackia franzi*. However, for both species the morphogenesis is known, clearly demonstrating that *C. halophila* has caudal cirri whereas they are lacking in *N. franzi*. Further, anlage II forms 3–4 cirri on average (middle frontal cirrus not included) in *N. franzi* against usually only one in *C. halophila*. Besides the morphological differences, *Neowallackia franzi* and *C. halophila* inhabit different soil types and obviously live in various biogeographic regions (non-saline soils in

Holarctis vs. saline soils in Australia; Blatterer & Foissner 1988, Foissner 1998). Thus, synonymy is very unlikely.

According to Eigner (1999, p. 46), the present species is closely related to *Orthoamphisiella stramenticola* Eigner & Foissner, 1991 (as already supposed by Eigner 1995; see above), *O. grelli* Eigner & Foissner, 1993, and *Gonostomum gonostomoidum* (Hemberger, 1982) Berger, 1999. However, as already discussed in a previous paragraph, *Orthoamphisiella* lacks, inter alia, the characteristic gonostomatid oral apparatus indicating that *G. franzi* does not belong to this genus. *Gonostomum gonostomoidum* is a true *Gonostomum* because it has transverse cirri and caudal cirri (p. 158). Further, the cirral pattern is identical with that of an 18-cirri hypotrich, except that some transverse cirri are lacking and anlage VI does not form four, but distinctly more cirri (see Fig. 25a for details).

The preceding discussion demonstrates that none of the previous generic assignments (*Gonostomum*, *Kahliella*, *Orthoamphisiella*) of *G. franzi* is well founded. A classification in *Wallackia*, briefly mentioned by Foissner (1982) and discussed in detail by Foissner et al. (2002), is also dissatisfactory because of several reasons (Berger & Foissner 1988, Foissner et al. 2002): (i) proter's anlage I is not formed de novo as in *Wallackia bujoreani*, but from the parental paroral; and (ii) no long primordium – splitting into opisthe's anlage I and II – is formed. A further distinct difference is the lack of caudal cirri in *G. franzi*, whereas these cirri are long and shaped like a Pasteur pipette in *Wallackia*. By contrast, the gonostomatid oral apparatus and the formation of the frontal-ventral cirri from five anlagen in *Wallackia* and *G. franzi* indicate a sistergroup relationships of these two taxa, supposed that in both taxa the same anlage (IV?, V?, VI?) is lacking. The loss of the caudal cirri, admittedly a rather simple feature, in *G. franzi* and two very similar species is interpreted as apomorphy of the new genus *Neowallackia*. For detailed comparison of *N. franzi* with *N. ghangriai*, see p. 295.

Morphology: The following chapter is mainly based on the original description (two terrestrial populations from the Austrian Central Alps), which is rather comprehensive (Foissner 1982). It is supplemented with some data of the population studied by Berger & Foissner (1988) to describe the cell division (a limnetic population from the Austrian Northern Alps). All populations agree very well.

Body size 100–130 × 28–40 µm, length:width ratio of live specimen shown in Fig. 52a about 3.9:1, ratio after protargol impregnation about 3.4:1 (Table 20). Body outline rather variable, usually elongate oval, rarely more or less distinctly sigmoidal; anterior and posterior end broadly to narrowly rounded (Fig. 52a, c). Rather sensitive against coverglass pressure. Body usually slightly sigmoidal in lateral view,

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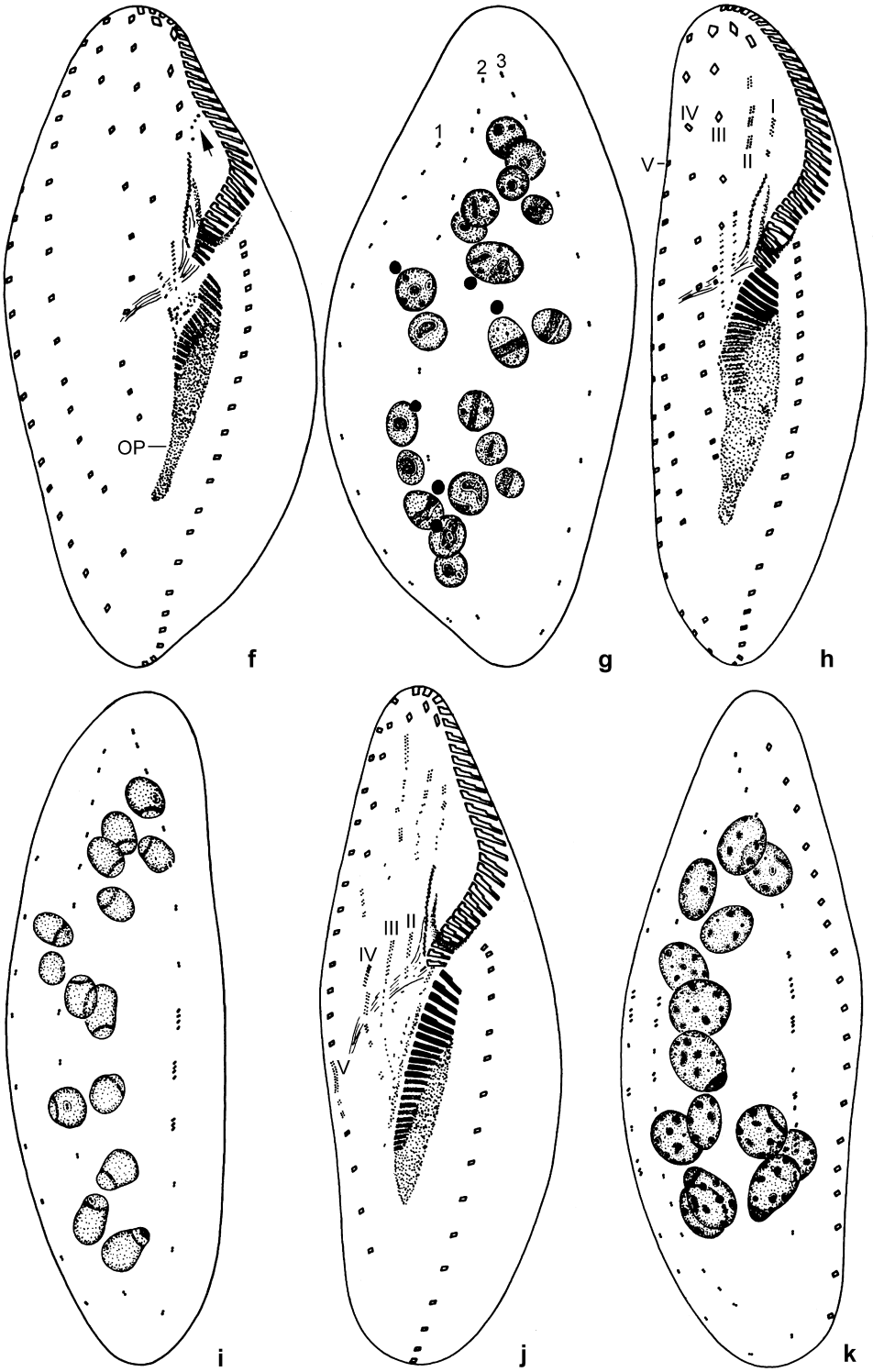
Fig. 53f–k *Neowallackia franzi* (from Berger & Foissner 1988. Protargol impregnation). Infraciliature of ventral (f, h, j) and dorsal (g, i, k) side and nuclear apparatus of early (f, g) and middle (h–k) dividers, f, g = 104 µm, h, i = 109 µm, j, k = 117 µm. Arrow in (f) marks parental paroral. Note that dorsal kinety formation commences both for the proter and the opisthe in about mid-body, that is, the two anlagen per kinety originate from a single primordium or two very narrowly spaced primordia (i, k). OP = oral primordium, I–V = frontoventral rows, respectively, anlagen, 1–3 = dorsal kineties. Page 281. →


OP
1
2
3
IV
III
II
I
V
f
g
h
i
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k

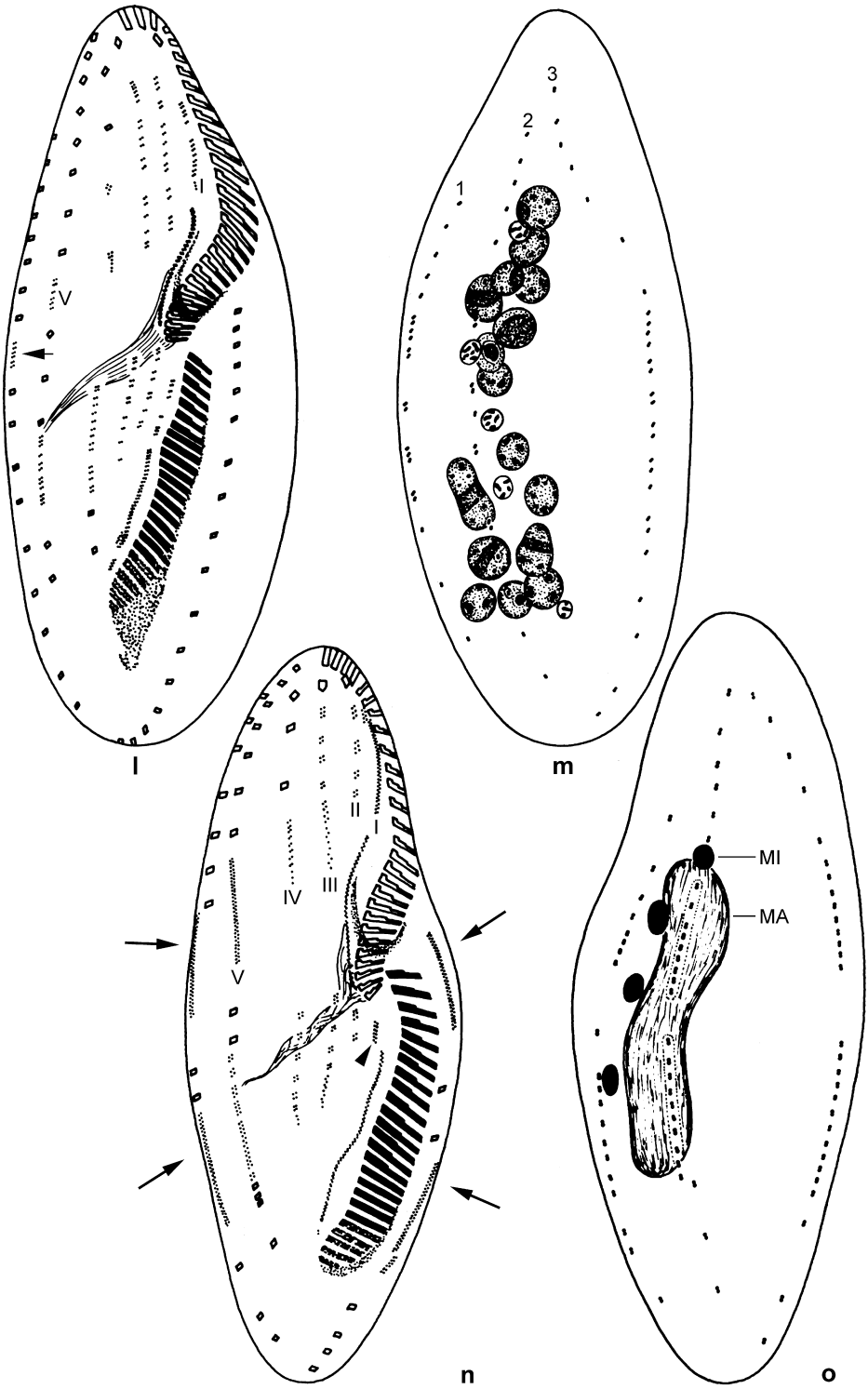
about 2–3:1 flattened dorsoventrally (Fig. 52b). 7–17, usually 11 or 12 globular macronuclear nodules, most of them arranged left of midline, in life about 7 × 5 µm, with moderate number of small chromatin bodies. Several irregularly distributed spherical micronuclei (Fig. 52a, e, f). Contractile vacuole near left body margin slightly ahead of mid-body, during diastole with canal extending anteriorly. Cytopyge on right body margin near rear cell end, faecal balls compact, yellowish (Fig. 52c). Pellicle colourless and flexible. Specific cortical granules lacking. Cytoplasm colourless, packed with tiny colourless granule (bacteria?) and few, 1–3 µm-sized, slightly yellowish crystals, which are often accumulated in posterior body portion so that specimens are dark at low magnification. Food vacuoles about 8 µm across. Movement fast, gliding, can closely attach to soil particles.

Oral apparatus as in *Gonostomum* (for review, see p. 15 and Berger 1999), that is, adoral zone commences at anterior end of cell, extends along left cell margin, and posterior portion curves rather abruptly obliquely backwards (Fig. 52a, d). Adoral zone occupies 40–45% of body length on average in protargol-impregnated specimens (Table 20), but only about 33% in life (36% in specimen illustrated). Buccal area flat and narrow. Paroral and endoral confused in original description and by Berger & Foissner (1988). Paroral mentioned, but not illustrated by Foissner (1982); single-rowed and about 3 µm long, according to Berger & Foissner (1988) composed of only three basal bodies (Fig. 52a), arranged ahead of endoral which is about 12 µm long, double-rowed, and extends from buccal vertex anteriorly (Fig. 52d, f, 53a). Pharyngeal fibres long, well recognisable in life.

Cirral pattern as shown in Fig. 52d, f, 53a, reminiscent of *Wallackia*. Frontal cirri not enlarged and thus difficult to distinguish from distal adoral membranelles and/or frontoventral cirri in life. Leftmost frontal cirrus slightly behind level of other two frontal cirri according to Fig. 53a. Usually five frontoventral cirral rows[1] (including leftmost frontal cirrus; row II sometimes lacking in specimens studied by Foissner 1982). Row II obviously homologous to buccal cirral row, rearmost cirrus of this row, however, distinctly ahead of anterior end of endoral and terminating at 11% (type population) and 22% (Schlossalm population) of body length on average (Table 20). Row III composed of five or six cirri on average, terminates at 35% and 31% (Table 20). Rows IV and V extend distinctly beyond buccal vertex (Fig. 52d, 53a), that is, terminate at 53% and 55%, respectively, 81% and 83% (Table 20). Rearmost cirrus of row V sometimes clearly separated from the cirrus lying ahead of

Fig. 53l–o *Neowallackia franzi* (from Berger & Foissner 1988. Protargol impregnation). Infraciliature of ventral (l, n) and dorsal (m, o) side and nuclear apparatus of middle dividers, l, m = 110 µm, n, o = 95 µm. Arrow in (l) marks right marginal row primordium of proter. Arrowhead in (n) denotes leftmost frontal cirrus of opisthe, arrows mark marginal row primordia. The macronuclear nodules fuse, as is usual for most hypotrichs, to a single mass during cell division. Parental structures white, new black. MA = fused macronucleus, MI = micronucleus, I–V = frontoventral rows/anlagen, 1–3 = dorsal kineties. Page 281. →

[1] I do not know which (IV? V? VI?) of the ordinary six (I–VI) anlagen/cirral rows is lacking. For simplicity, the five anlagen/rows present are termed I–V.


I
V
l
3
2
1
m
II
I
IV
III
V
n
MI
MA
o

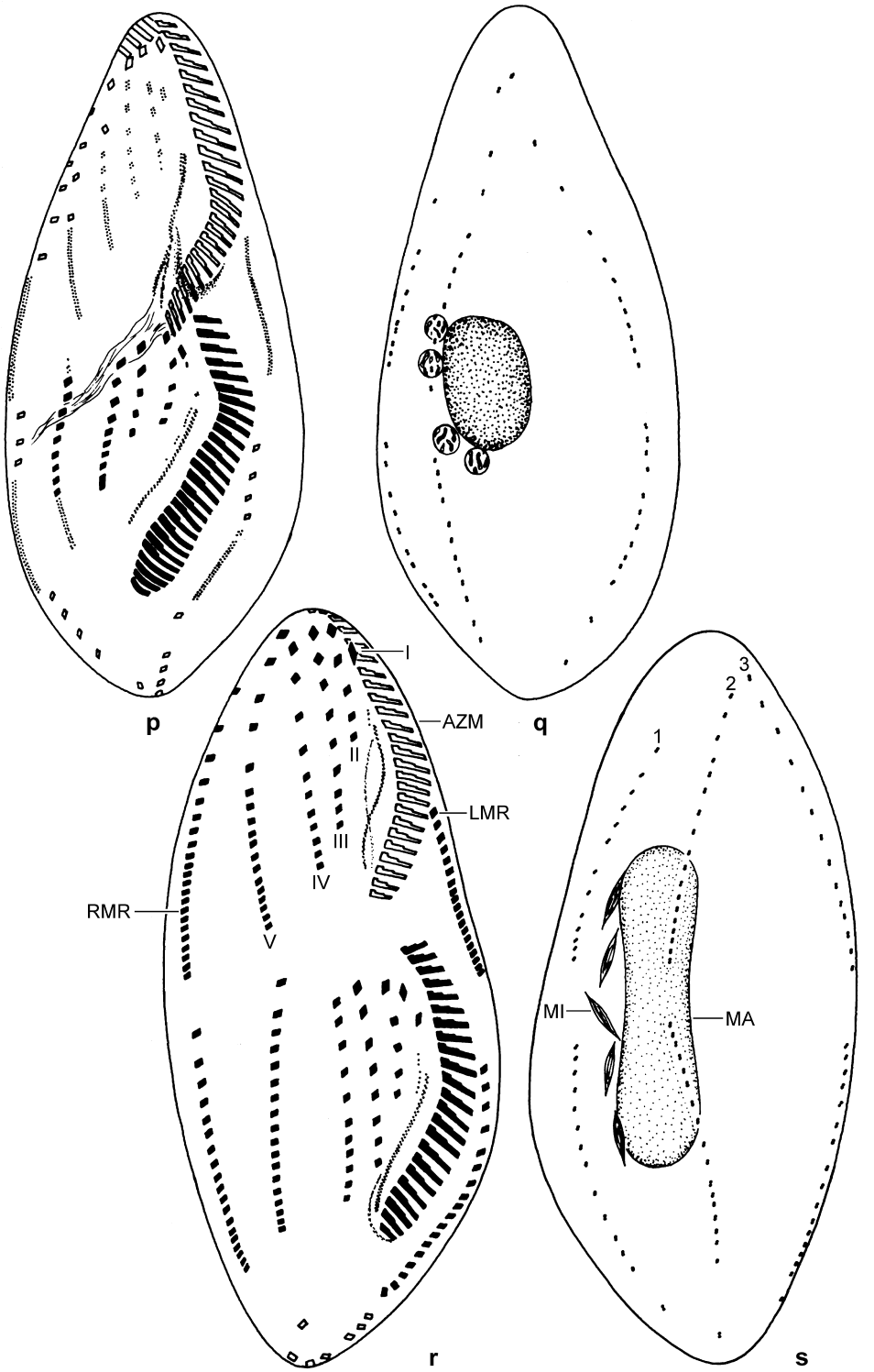
it. Transverse cirri lacking. Right marginal row more or less distinctly shortened anteriorly, anterior portion extends dorsolaterally, ends slightly subterminally and is almost continuous with left marginal row, which commences left of proximal portion of adoral zone; rearmost cirri of left marginal row must not be misinterpreted as caudal cirri, which are lacking.

Dorsal cilia about 4 µm long in life, invariable arranged in three kineties; kinety 1 distinctly shortened anteriorly, kineties 2 and 3 commence near anterior cell end; all kineties extend to near rear cell end. Bristles in kineties 1 and 2 about equally spaced, in kinety 3 of populations studied by Foissner (1982) distance among bristles in posterior portion about twice as large as anteriorly. Caudal cirri and dorsomarginal kinety lacking (Fig. 52e; see cell division).

Cell division (Fig. 53a–w): This part of the life cycle is described in detail by Berger & Foissner (1988). It commences with the formation of a long and narrow oral primordium between the left marginal row and the frontoventral row IV, obviously without contact to any parental cirri (Fig. 53c). In the next stage, a row of basal bodies from the right anterior end of the oral primordium migrates in an anteriad direction (Fig. 53e). Later, two streaks are recognisable (Fig. 53f). The right one is in line with frontoventral row III, which appears disorganised in the posterior portion, indicating that one or two cirri have been incorporated in this streak. The parental paroral is slightly stretched, which is the first sign of its modification to an anlage (Fig. 53f). All cirri of frontoventral row II, except for the frontal cirrus, are disorganised. Two streaks are present at the level of the buccal vertex (Fig. 53h).

The cirri of the parental frontoventral row III (except the frontal cirrus), the middle and rear part of frontoventral row IV, and some cirri behind to the middle portion of frontoventral row V are modified to anlagen in the next stage. The undulating membranes primordium of the opisthe is formed to the right of the oral primordium (Fig. 53j). Cell division continues with the formation of a second anlage in frontoventral row V and the origin of the anterior right marginal row primordium (Fig. 53l). In total, only five (I–V) frontal-ventral cirri anlagen are formed (e.g., Fig. 53r), which agrees with *Wallackia* (e.g., Fig. 41m). Which (IV? V? VI?) of the six ordinary (I–VI) frontal-ventral cirri anlagen is lacking is not known. For sake of simplicity the five anlagen are termed I–V. All ventral and marginal primordia are recognisable in the next stage (Fig. 53n). The new frontal cirri and some cirri of the new rows II, III, and IV are already segregated. The paroral and endoral of the proter (anlage I) and the parental endoral are clearly separated.

Fig. 53p–s *Neowallackia franzi* (from Berger & Foissner 1988. Protargol impregnation). Infraciliature of ventral (p, r) and dorsal (q, s) side and nuclear apparatus of a late (p, q) and a very late (r, s) divider, p, q = 120 µm, r, s = 95 µm. Note that *Neowallackia franzi* produces only five frontoventral primordia, that is, one (IV? V? VI?) of the ordinary six anlagen is lacking. Parental structures white, new black. AZM = parental adoral zone (retained for proter), LMR = new left marginal row of proter, MA = fused macronucleus, MI = dividing micronucleus, RMR = new right marginal row of proter, I–V = frontoventral anlagen, 1–3 = dorsal kineties. Page 281. →


p
q
I
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II
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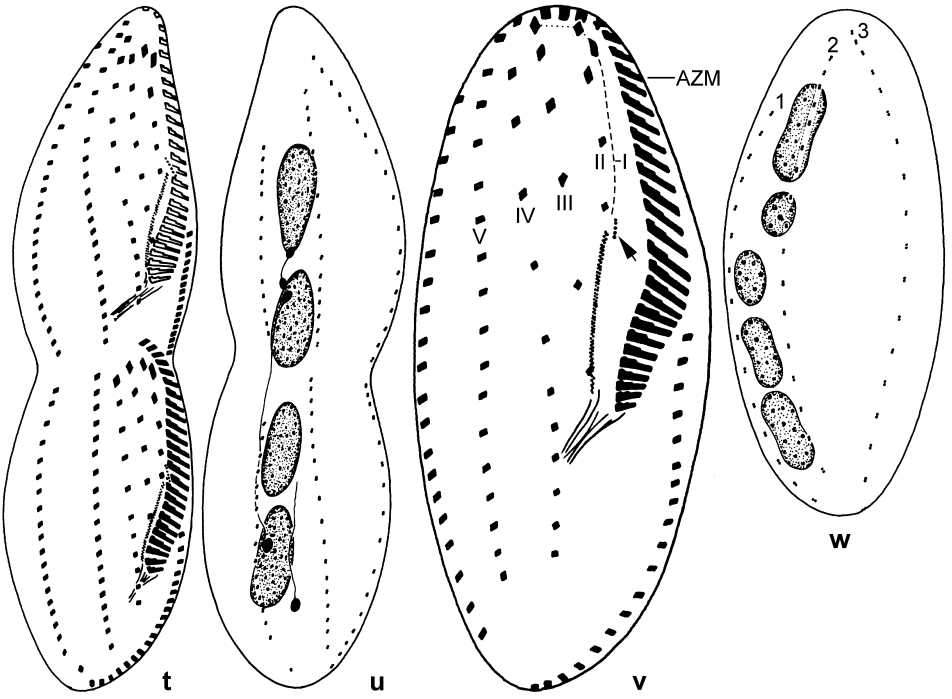

Fig. 53t–w *Neowallackia franzi* (from Berger & Foissner 1988. Protargol impregnation). **t, u:** Infraciliature of ventral and dorsal side and nuclear apparatus of a very late divider, 139 µm. Note that no caudal cirri are formed at the end of the dorsal kineties. **v, w:** Infraciliature of ventral and dorsal side and nuclear apparatus of an opisthe, 80 µm. Arrow in (v) marks paroral, which is composed of only few basal bodies/cilia in *N. franzi*. The macronucleus divides several times until the species-specific number of 11 or 12 nodules is present. Parental structures white, new black. AZM = adoral zone of membranelles, I–V = frontoventral rows, 1–3 = dorsal kineties. Page 281.

Figure 53p shows a late divider with the final number of adoral membranelles in the new adoral zone. The anlage for the new paroral is recognisable right to the anterior end of the endoral. The parental adoral zone is retained for the proter. Cytokinesis and displacement of cirri occur in very late dividers and postdividers (Fig. 53r, t, v). No peculiarities are recognisable during these processes.

The morphogenesis of the dorsal side proceeds in the *Gonostomum* pattern (Berger & Foissner 1997, Berger 1999). Few basal body pairs commence with the proliferation in the middle portion of dorsal kinety 3 (Fig. 53i). Somewhat later, proliferation of basal bodies occurs in all dorsal kineties at two sites, only indistinctly separated by one or two parental basal body pairs (Fig. 53k). The primordia of the dorsal bristle rows are elongated (Fig. 53m). Later, the anlagen of the filial products separate (Fig. 53o, q). No caudal cirri are formed at the end of the dorsal kineties (Fig. 53s, u, w).

Table 20 Morphometric data on *Neowallackia franzi* (fr1, from Foissner 1982, type population; fr2, from Foissner 1982, Schlossalm population), *Neowallackia ghangriai* (gha, from Kamra et al. 2008), and *Neowallackia petergofi* (pet, original data of type population [Alekperov 2005] kindly supplied by Ilham Alekperov)

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Body, length	fr1	72.1	73.0	8.0	2.7	11.8	54.0	80.0	9
	fr2	69.6	68.0	5.9	1.8	8.5	60.0	84.0	11
	gha	72.2	–	4.0	–	5.5	66.6	77.9	10
	pet [e]	51.5	51.0	5.6	1.8	11.0	45.0	60.0	10
Body, width	fr1	21.1	21.0	2.9	1.0	13.7	17.0	25.0	9
	fr2	20.4	20.0	2.0	0.6	9.9	17.0	25.0	11
	gha	21.2	–	1.5	–	7.1	18.7	23.8	10
Body length:width, ratio	gha	3.4	–	0.2	–	6.5	2.9	3.6	10
Adoral zone of membranelles, length	fr1	32.8	33.0	1.9	0.6	5.9	29.0	35.0	9
	fr2	28.2	28.0	1.7	0.5	6.0	25.0	30.0	11
	gha	32.6	–	1.5	–	4.7	29.5	34.0	10
Anterior body end to paroral, distance	gha	16.3	–	0.6	–	3.4	15.6	17.3	10
Anterior body end to endoral, distance	gha	18.3	–	0.5	–	2.6	17.8	19.3	10
Anterior body end to rear end of fronto-ventral row II, distance	fr1	7.6	8.0	1.9	0.6	25.8	4.0	11.0	9
	fr2	15.0	15.0	0.8	0.3	5.7	14.0	17.0	11
Anterior body end to rear end of fronto-ventral row III, distance	fr1	25.1	25.0	4.5	1.5	17.7	20.0	35.0	9
	fr2	21.5	20.0	4.6	1.4	21.5	16.0	31.0	11
Anterior body end to rear end of fronto-ventral row IV, distance	fr1	38.1	37.0	5.7	1.9	14.9	29.0	45.0	9
	fr2	38.0	38.0	4.2	1.3	11.2	31.0	45.0	11
Anterior body end to rear end of fronto-ventral row V, distance	fr1	58.3	62.0	10.0	3.3	17.1	40.0	68.0	9
	fr2	57.9	57.0	7.7	2.3	13.3	44.0	69.0	11
Macronuclear nodule, length [d]	fr1	5.5	5.3	1.5	0.5	28.0	4.0	8.0	9
	fr2	6.3	6.6	2.3	0.7	36.1	4.0	10.6	11
	gha	4.1	–	0.8	–	19.2	3.2	5.4	10
Macronuclear nodule, width [d]	fr1	3.6	4.0	0.6	0.2	17.2	2.6	4.0	9
	fr2	4.0	4.0	0.6	0.2	13.9	2.8	5.3	11
Macronuclear nodules, number	fr1	11.0	12.0	2.7	0.9	25.0	7.0	14.0	9
	fr2	12.5	12.0	2.5	0.8	19.9	8.0	17.0	11
	gha	18.0	–	3.0	–	16.8	3.0	21.0	10
Anteriormost micronucleus, length	gha [d]	1.5	–	0.2	–	10.3	1.2	1.8	10
Micronuclei, number	gha	4.9	–	0.7	–	15.0	4.0	6.0	10
Paroral, length	gha	1.6	–	0.2	–	11.7	1.3	2.1	10
Paroral kinetids, number	gha	3.0	–	0.5	–	15.7	2.0	4.0	10
Paroral, distance between basal bodies	gha	0.3	–	0.0	–	10.3	0.2	0.3	10
Adoral membranelles, number	fr1	25.4	25.0	0.8	0.3	3.3	24.0	27.0	9
	fr2	28.1	29.0	2.1	0.6	7.7	24.0	30.0	11
	gha	29.4	–	3.8	–	12.9	24.0	37.0	10
	pet [b]	56.5	58.0	4.0	1.3	7.1	50.0	60.0	10
Frontal cirri, number	pet	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
Frontoventral row I, number of cirri [c]	gha	1.0	–	0.0	–	0.0	1.0	1.0	10
Frontoventral row II, number of cirri [c]	fr1	2.8	3.0	0.4	0.1	15.0	2.0	3.0	9
	fr2	3.9	4.0	0.5	0.2	13.2	3.0	5.0	11
	gha	4.0	–	0.0	–	0.0	4.0	4.0	10
Frontoventral row III, number of cirri [c]	fr1	5.8	6.0	0.6	0.2	10.9	5.0	7.0	9
	fr2	5.5	5.0	1.4	0.4	25.9	4.0	9.0	11
	gha	7.0	–	0.5	–	6.7	4.0	6.0	10
	pet	4.0	4.0	0.0	0.0	0.0	4.0	4.0	10

Table 20 Continued

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Frontoventral row IV, number of cirri	fr1	9.9	10.0	1.4	0.5	13.8	7.0	12.0	9
	fr2	10.5	10.0	1.4	0.4	13.0	9.0	13.0	11
	gha	11.0	–	0.7	–	6.1	10.0	12.0	10
	pet	6.7	7.0	0.5	0.2	7.2	6.0	7.0	10
Frontoventral row V, number of cirri	fr1	15.7	16.0	1.2	0.4	8.0	13.0	17.0	9
	fr2	19.9	20.0	2.1	0.6	10.6	17.0	24.0	11
	gha	21.9	–	0.6	–	2.6	21.0	23.0	10
	pet	8.7	9.0	0.5	0.2	5.6	8.0	9.0	10
Right marginal row, number of cirri	fr1	18.7	19.0	2.0	0.7	10.7	15.0	22.0	9
	fr2	24.7	25.0	3.3	1.0	13.5	20.0	32.0	11
	gha	23.5	–	1.4	–	5.8	21.0	25.0	10
	pet	18.6	19.0	0.7	0.2	3.8	17.0	19.0	10
Left marginal row, number of cirri	fr1	18.9	18.0	2.8	0.9	15.1	15.0	25.0	9
	fr2	20.9	21.0	2.2	0.7	10.5	18.0	25.0	11
	gha	19.1	–	2.0	–	10.3	15.0	22.0	10
Dorsal kineties, number	fr1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	9
	fr2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	gha	3.0	–	0.0	–	0.0	3.0	3.0	10
Kinetids in dorsal kinety 1, number	gha	11.4	–	2.9	–	25.6	9.0	18.0	10
Kinetids in dorsal kinety 2, number	gha	14.5	–	1.4	–	9.4	12.0	16.0	10
Kinetids in dorsal kinety 3, number	gha	16.3	–	2.2	–	13.3	3.0	21.0	10

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known), SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated (fr1, fr2, gha) or wet silver nitrate-impregnated (pet) specimens.

[b] Rather high values for such a small species; revisal recommended (see remarks).

[c] Frontal cirri not included (fr1, fr2), respectively, included (gha).

[d] Macronuclear nodule (anterior? posterior?) or micronucleus measured not indicated. For gha the diameter is given.

[e] From life.

The macronuclear nodules show replication bands (Fig. 53d, g, i). As is usual, the nodules fuse to a single mass and divide into the species-specific number in later stages and in postdividers (Fig. 53k, m, o, q, s, u, w).

Occurrence and ecology: *Neowallackia franzi* prefers terrestrial habitats, but is also reliable recorded from freshwater (Foissner 1987a, p. 123; 1998, p. 206; Berger & Foissner 1988). Common in Austrian soils and possibly confined to the Holarctis (Foissner & Foissner 1988, p. 88; Foissner 1998, p. 206). The type locality is in the "Guttal" near the Großglockner-Hochalpenstrasse, a famous alpine road in Salzburg, Austria, where Foissner (1982) discovered it in the soil of an alpine pasture at an altitude of 1900 m. Foissner (1982) found it also in several other terrestrial sites of the Großglockner-area (for autecological data, see Foissner 1981; see also Krainer 1999, p. 668), in the Schlossalm-area near the village of Bad Hofgastein (Salzburg; eco-

logical data, see Foissner 1985, p. 83 and Foissner & Peer 1985, p. 40), and in the Tullnerfeld-region, Lower Austria (ecological data, see Foissner et al. 1985, p. 108). Berger & Foissner (1988) discovered their population in a small, alpine pond near the village of Lunz, Lower Austria; specimens were cultured in Eau de Volvic with some squashed wheat grains to support microbial growth.

Records not substantiated by morphological data: in experiments on soil compaction and the effect of fertilisers and lime on an alpine pasture carried out in the Schlossalm area, Salzburg, Austria (Berger et al. 1985a, p. 107; 1986, p. 268); soil from a location of an abandoned textile mill in the city of Nordhorn, Germany (Niebuhr 1989, p. 81; identified by W. Foissner); various soils in Slovakia (Tirjaková 1988, p. 499; 2005, p. 21).

Food vacuoles contain bacteria, heterotrophic flagellates, and inorganic soil particles (Fig. 52a; Foissner 1982). Biomass of 10^6 specimens about 30 mg (Foissner 1987a, p. 123; 1988, p. 206).

Neowallackia ghangriai (Kamra, Kumar & Sapra, 2008) comb. nov.

(Fig. 54a–c, Table 20)

2008 ***Paragonostomum ghangriai* sp nov** [1] – Kamra, Kumar & Sapra, Indian J. Microbiol., 48: 378, Fig. 4a–d, 11a–h, Table 3 (Fig. 54a–c; original description; one protargol slide is deposited in the Natural History Museum, London).

Nomenclature: The species-group name *ghangriai* refers to the settlement Ghangria located in the periphery of the Valley of Flowers National Park, where the species was discovered (Kamra et al. 2008). No accession number for the type slide is given in the original description.

Remarks: Kamra et al. (2008) did not compare their species with *Neowallackia franzi* although they have the same cirral pattern. The only difference concerning this feature are the caudal cirri which are present in *P. ghangriai*, but lacking in *N. franzi*. However, from *N. franzi* it is known that the rearmost cirri of the left marginal row can be very easily misinterpreted as caudal cirri. And indeed, a photomicrograph in Kamra et al. (2008; their Fig. 11f) rather clearly demonstrates that the "caudal cirri" of *P. ghangriai* are the rearmost left marginal cirri. Thus, the Indian species is also transferred to *Neowallackia*. The only true difference between the type species and *N. ghangriai* consists in the cortical granulation. According to Foissner (1982) and Berger & Foissner (1988), cortical granules are lacking in *N.*

[1] Kamra et al. (2008) provided the following diagnosis: Body elongated without a tail; mean size in vivo of non dividers 75 × 22 µm, protargol stained cells range between 67–78 µm × 19–24 µm; cortical granules colourless and scattered; extrusomes present; single contractile vacuole, 13–21 macronuclei, 4–6 micronuclei; AZM 40% of body length, PM 2–4 cilia, sometimes bipartite, EM made of tightly packed cilia; 5 fronto-ventral rows (FV1–5), transverse cirri absent; 1 LMC row and 1 RMC row; 3DKs and 3 CCs; cirri long; ontogenesis in *Gonostomum* pattern.

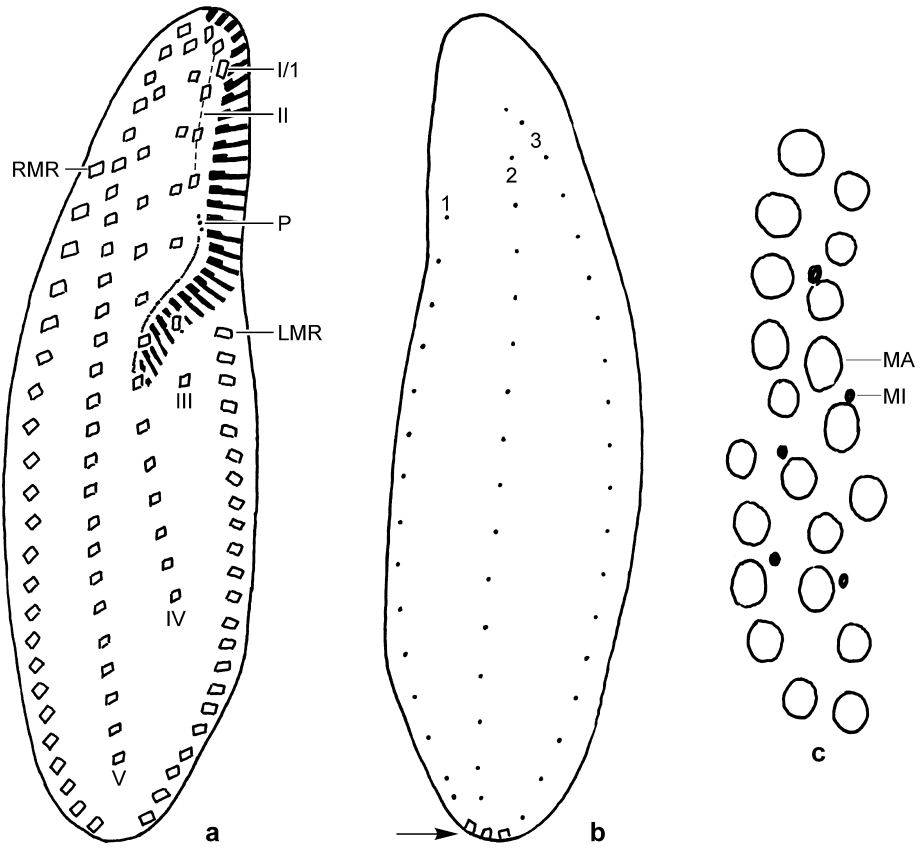

Fig. 54a–c *Neowallackia ghangriai* (after Kamra et al. 2008. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 73 µm. Arrow in (b) marks rearmost left marginal cirri at rear end of cell (likely misinterpreted as caudal cirri by Kamra et a. 2008; details, see text). LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = anterior end or right marginal row, I/1 = left frontal cirrus, I–V = frontoventral cirri rows/anlagen, 1–3 = dorsal kineties. Page 295.

franzi, whereas *N. ghangriai* has colourless granules. However, their number is low and they do not stain with protargol so that they can be easily overlooked. In addition to the cortical granules, *Neowallackia ghangriai* has extrusomes, which have no particular arrangement. They are 1.6–2.1 × 0.6–0.7 µm in size and stain with protargol (Kamra et al. 2008, p. 378, 379, 385). Thus, synonymy of *N. franzi* and *N. ghangriai* can be excluded, at least at the present state of knowledge. The species differ also in the average number of macronuclear nodules (11–12 vs. 18; Table 20). Further populations of both species from their type localities (Austria; India) should be studied to confirm the data. Interestingly, both taxa have their type localities in montane soils.

Wallackia species, which also have distinct extrusomes, differ from *N. ghangriai* by the two macronuclear nodules and the presence of very prominent caudal cirri (p. 206). In addition, their paroral is composed of more cilia. Although the extrusomes of the present species are reminiscent of *Wallackia*, I strongly doubt that it belongs to this genus because some other important details (few paroral cilia; increased number of macronuclear nodules; caudal cirri lacking) agree very well with that of *N. franzi*.

Neowallackia ghangriai and *N. franzi* are, according to the sparse data, clearly separated geographically (India vs. Europe). The type species, for example, was not recorded during detailed surveys of Australian and Namibian soils (Blatterer & Foissner 1988, Foissner et al. 2002a), indicating that it has a restricted distribution.

Morphology: Body size of live specimens 75 × 22 µm on average. Body elongate and slightly sigmoidal, with posterior end somewhat more broadly roundly than anterior one. Nuclear apparatus composed of 13–21, on average 18 globular to slightly ellipsoidal nodules and 4–6 globular micronuclei. Contractile vacuole just below level of buccal vertex, somewhat left of body midline. Cortical granules colourless, scanty dispersed; do not stain with protargol; size not indicated. In addition to the cortical granules, extrusomes are present "throughout the body in no particular arrangement"; stain with protargol and then they are 1.6–2.1 × 0.6–0.7 µm in size (Fig. 11h in Kamra et al. 2008). Fat globules mainly concentrated in posterior body region. Movement fast, jerky, "sometimes rolling over sideways and lengthwise", that is, likely sometimes rotating about main body axis.

Adoral zone gonostomatid, occupies about 45% of body length, composed of 29 membranelles on average (Fig. 54a). Paroral very short because made up of usually 2–4 widely spaced cilia only; sometimes in bipartite arrangement, and one specimen with six paroral cilia (Fig. 54a). Endoral extends from paroral to buccal vertex, composed of narrowly spaced cilia.

Cirri pattern as in *N. franzi* (Fig. 54a), that is, frontal-ventral cirri arranged in five rows, including row/anlage I forming only leftmost frontal cirrus. Average number of cirri increases from row I to V (frontal cirri included): 1 (only left frontal cirrus); 4; 7; 11; 22. Transverse cirri lacking. Right marginal row distinctly shortened anteriorly, commences at 19% of body length in specimen illustrated; terminates near rear end of cell. Left marginal row begins left of proximal adoral membranelles, terminates, according to Fig. 54a, about at same level as right marginal row; however, note that Fig. 54a is very likely incorrect in this respect because Fig. 11f in Kamra et al. (2008) rather clearly shows that the rear end of the left marginal row extends onto the dorsal surface feigning caudal cirri. Of course, ontogenetic data are needed to confirm (or disprove) my interpretation.

Dorsal bristles arranged in three kineties; kinety 1 – as in type species – distinctly shortened anteriorly. The three caudal cirri described by Kamra et al. (2008) are, very likely, misinterpreted left marginal cirri (see previous paragraph; Fig. 54b). Length of bristles not mentioned, but according to Fig. 11g in the original description roughly of ordinary length, that is, about 2–4 µm.

Cell division: According to Kamra et al. (2008), ontogenesis is in *Gonostomum* pattern. Unfortunately, not details have been provided.

Occurrence and ecology: The type locality of *N. ghangriai* is the Valley of Flowers National Park (30°41'–30°48'N 79°33'–79°46'E), Himalayan region, India. The soil samples were taken close to the settlement Ghangria at the periphery of the park; no further details given. Food not mentioned.

Neowallackia petergofi (Alekperov, 2005) comb. nov.
(Fig. 55a, b, Table 20)

2005 ***Trachelochaeta petergoffii* sp. n.** – Alekperov, Atlas of free-living ciliates, p. 218, Fig. 69.1–2, Plate 22.1 (Fig. 55a, b; original description; no formal diagnosis provided; type slides ["S-P. -No8"] likely deposited in the private collection of Ilham Alekperov).

2005 ***Trachelochaeta petergofi* sp. n.** – Alekperov, Atlas of free-living ciliates, p. 287 (see nomenclature).

Nomenclature: The species-group name *petergofi* refers to the site (Petergof Park near St. Petersburg, Russia) where the species was discovered (Alekperov 2005). Alekperov (2005) introduced two original spellings of the species-group name, namely *petergoffii* and *petergofi*. I fix, as first reviser, *petergofi* (composite of the proper name Petergof and the masculine genitive ending *-i*) as correct original spelling (Hentschel & Wagner 1996, p. 39; ICZN 1999, Article 31).

Remarks: This species is very similar to *Neowallackia franzi* strongly indicating a close relationship. Thus, *Trachelochaeta petergofi* is also classified in *Neowallackia*. The major differences between the two species are in the number of macronuclear nodules (2 vs. about 11 on average) and the number of buccal cirri (1 vs. 3 or 4; frontal cirrus formed by anlage II not included). The number of cirri in the cirral rows II–V is distinctly lower in *N. petergofi* than in *N. franzi*, what corresponds with the different body size (around 50 µm vs. 100–130 µm). By contrast, the number of adoral membranelles is conspicuously higher in *N. petergofi* than in *N. franzi* (50–60 vs. 24–30; Table 20), indicating a misobservation in *N. petergofi* due to the suboptimal preparation method (see Alekperov 2005, p. 287, Fig. 1). *Gonostomum terrestre*, which has the same type locality as *N. petergofi*, resembles the present species (Fig. 26a, b). Whether or not the differences (transverse cirri present vs. absent; 5 dorsal kineties vs. 3) are correct and stable has to be checked by detailed redescriptions of both species.

Morphology: The original description is in Russian. Ilham Alekperov sent me an English summary of the description and some unpublished morphometric data (Table 20).

Body length in life about 45–60 µm; prepared specimen illustrated 37 × 17 µm (Fig. 55a), body outline of prepared specimen thus elliptical. Two macronuclear nodules distinctly separated from each other; anterior nodule illustrated about 6.0 × 3.5 µm (Fig. 55b). One small globular micronucleus attached to each macronuclear

nodule (Fig. 55b). Contractile vacuole near anterior end of left marginal row. Cortical granules lacking. Cytoplasm, nutrition, and movement likely without peculiarities.

Oral apparatus obviously in *Gonostomum*-pattern (see *N. franzi* for details). However, details of undulating membranes hardly recognisable in illustration (Fig. 55a); structure, shape, and arrangement likely very similar to that of type species. Number of adoral membranelles (50–60; Table 20) probably distinctly overestimated (see remarks). Adoral zone occupies about 54% of body length in specimen illustrated (Fig. 55a).

Cirral pattern basically as in type species (Fig. 55a). Frontal cirri slightly enlarged, left one somewhat displaced posteriad. Invariably one buccal cirrus, obviously ahead of endoral. Frontoventral row III constantly composed of four cirri, ends about at level of anterior end of endoral. Frontoventral row IV terminates about at level of buccal vertex; row V extends to about 66% of body length in specimen illustrated (Fig. 55a). Transverse cirri lacking. Right marginal row terminates near rear cell end. Left marginal row commences somewhat ahead of level of buccal vertex, terminates, like right row, near rear body end. Silverline system of ventral side fine-meshed, as is usual (Fig. 55a).

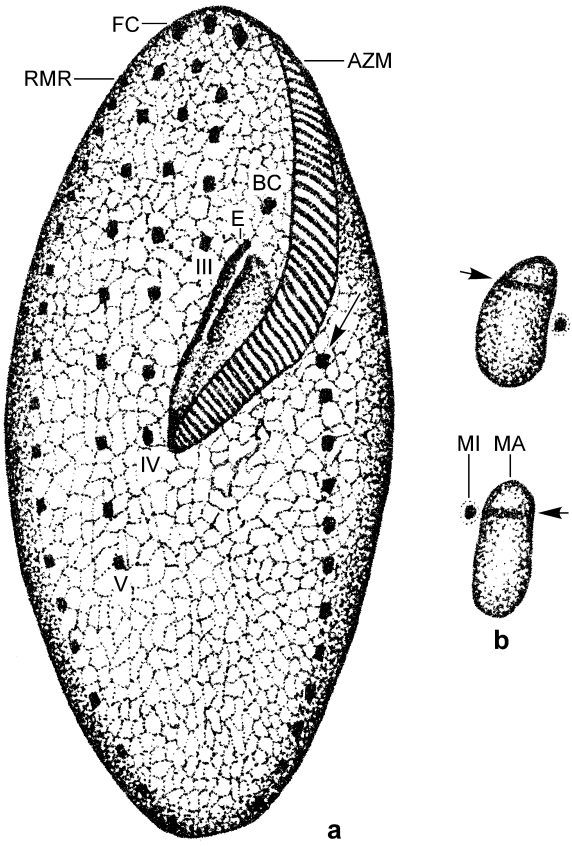

Fig. 55a, b *Neowallackia petergofi* (from Alekperov 2005. Wet silver nitrate impregnation). Infraciliature of ventral side and nuclear apparatus, a = 37 µm. Arrow in (a) marks anterior end of left marginal row. Arrows in (b) denote the replication bands; note that the bands are at the anterior end in both nodules which is uncommon (misobservation?). AZM = adoral zone of membranelles (number of membranelles probably overestimated), BC = buccal cirrus, E = endoral?, FC = right frontal cirrus, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row, III–V = frontoventral rows. Page 298.

Dorsal bristles 5–7 µm long; arranged in three (more or less bipolar?) kineties. Caudal cirri lacking.

Occurrence and ecology: Likely confined to terrestrial habitats. Type locality of *N. petergofi* is the Petergof Park near the city of St. Petersburg (Russia) where Alekperov (2005) discovered it in soil. Also found in subalpine soils of Azerbaijan (I. Alekperov; pers. comm.). No further records published.

Incertae sedis in the Gonostomatidae

The following two genera (*Trachelochaeta* and *Circinella*) are difficult to assign to a certain higher taxon. I preliminary classify them in the gonostomatids because all other assignments are still less convincing.

Trachelochaeta Šrámek-Hušek, 1954

1954 ***Trachelochaeta* nov. gen.**[1] – Šrámek-Hušek, Arch. Protistenk., 100: 265 (original description). Type species (by original designation): *Trachelochaeta bryophila* Šrámek-Hušek, 1954.
1961 ***Trachelochaeta* Šrámek-Hušek** – Corliss, Ciliated Protozoa, p. 170 (classification of ciliates).
1972 ***Trachelochaeta* Šrámek-Hušek, 1954** – Borror, J. Protozool., 19: 15 (revision of hypotrichs).
1974 ***Trachelochaeta* Šrámek-Hušek, 1954** – Stiller, Annls hist.-nat. Mus. natn. hung., 66: 130 (classification of hypotrichs).
1974 ***Trachelochaeta* Šramek-Hušek** – Stiller, Fauna Hung., 115: 87 (revision of hypotrichs).
1975 ***Trachelochaeta*** – Corliss, Trans. Am. microsc. Soc., 94: 257 (classification of ciliates).
1975 ***Trachelochaeta* Šr.-Hušek** – Corliss, Trans. Am. microsc. Soc., 96: 137 (classification of ciliates).
1979 ***Trachelochaeta* Šramek-Hušek, 1954** – Jankowski, Trudy zool. Inst., Leningr., 86: 67 (catalogue of hypotrich genera).
1979 ***Trachelochaeta* Šrámek-Hušek, 1954** – Tuffrau, Trans. Am. microsc. Soc., 98: 526 (classification of hypotrichs).
1979 ***Trachelochaeta* Šrámek-Hušek, 1954** – Corliss, Ciliated Protozoa, p. 309 (classification of ciliates).
1982 ***Trachelochaeta* Šrámek-Hušek, 1954** – Hemberger, Dissertation, p. 44 (detailed revision of hypotrichs).
1983 ***Trachelochaeta* Šrámek-Husek, 1954** – Curds, Gates & Roberts, British and other freshwater ciliated protozoa, p. 416 (guide to freshwater genera).
1985 ***Trachelochaeta*** – Small & Lynn, Ciliophora, p. 455 (guide to ciliate genera).
1987 ***Trachelochaeta* Sramek-Husek, 1954** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (classification of hypotrichs).
1999 ***Trachelochaeta* Šrámek-Hušek, 1954** – Berger, Monographiae biol., 78: 894 (brief note on exclusion from oxytrichids).
2001 ***Trachelochaeta* Šrámek-Hušek 1954** – Aescht, Denisia, 1: 164 (catalogue of generic names of ciliates).
2001 ***Trachelochaeta* Šrámek-Hušek, 1954** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 89 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).
2002 ***Trachelochaeta* Srámek-Husek, 1954** – Lynn & Small, Ciliophora, p. 456 (guide to ciliate genera).

[1] Šrámek-Hušek (1954) provided the following diagnosis: Das neue Genus ähnelt durch die Verlagerung des Peristoms an die linke Schmalseite und durch zahlreiche Frontalcirren der Kahlschen Gattung *Trachelostyla* (1932), unterscheidet sich aber von ihr markant durch 2 geschlossene Ventralreihen, vier lange, gespreizte Caudalcirren, 2 Kernteile und gut entwickelte pulsierende Vakuole.

2006 ***Trachelochaeta* Šrámek-Hušek, 1954** – Berger, Monographiae biol., 85: 1212 (brief note on exclusion from urostyloids).
2007 ***Trachelochaeta* Sramek-Husek, 1954** – Jankowski, Ciliophora, p. 469 (revision of ciliates).
2008 ***Trachelochaeta* Šrámek-Hušek, 1954** – Berger, Monographiae biol., 88: 470 (brief note on exclusion from amphisiellids).
2008 ***Trachelochaeta* Šrámek-Hušek, 1954** – Lynn, Ciliated protozoa, p. 357 (revision of ciliates).

Nomenclature: No derivation of the name is given in the original description. *Trachelochaeta* is a composite of the Greek substantives *ho trachelos* (the neck) and *he chaite* (the bristle). The first part obviously refers to the neck-like narrowed anterior body portion. Whether the second part (*chaeta*) refers to a special group of cirri or bristles (e.g., caudal cirri, dorsal bristles; cirri and bristles on the "neck") or to the cirri and bristles in general in the sense of "ciliate" or "hypotrich" is not known. Feminine gender (Aescht 2001, p. 303).

Šrámek-Hušek (1954, p. 265) used the term "Genotyp" to fix *T. bryophila* as type species. According to the code, this term should never be used for this purpose (e.g., ICZN 1964, 1999, Recommendation 67A). However, since this is only a recommendation, the type fixation is by original designation and not primarily by monotypy as supposed by Borror (1972).

Characterisation (A = supposed apomorphy): Gonostomatidae (?) with anterior body portion distinctly narrowed (A?). Adoral zone gonostomatid. Undulating membrane pattern not known. Likely five frontoventral rows (left frontal cirrus included); rows II and III confined to oral area, form conspicuous cirral pairs; rows IV and V distinctly shortened anteriorly. Five transverse cirri. One right and one left marginal row. Prominent caudal cirri present. Dorsal kinety pattern not known.

Remarks: *Trachelochaeta*, with the single species *T. bryophila*, is a little known, but interesting taxon. Although based on live observations only, the organisation is basically well described (Fig. 56a). The arrangement of the cirri is reminiscent of *Wallackia*, because in both genera the left frontoventral rows (rows II and III) are confined to the oral area and their cirri form distinct pseudo-pairs. Likely because of these pairs, Stiller (1974, 1974a), Corliss (1977, 1979), Tuffrau (1979, 1987), and Curds et al. (1983) classified *Trachelochaeta* in the holostichids. However, in the urostyloids, to which the holostichids[1] belong, the cirral pairs form a characteristic zigzag pattern (Berger 2006a); further, the pairs are produced by many anlagen whereas in *Trachelochaeta* the pairs are formed from only two anlagen, presumed that ontogenesis proceeds as in *Wallackia*. This assumption, however, has to be confirmed by ontogenetic data from *Trachelochaeta bryophila*.

Šrámek-Hušek (1954) established *Trachelochaeta* in the Heterotricha, an inexplicable classification. In addition, he mentioned a similarity of *Trachelochaeta* and *Trachelostyla* (for review, see Berger 2008, p. 474). However, *Stichochaeta pediculiformis* Cohn, 1866, type species of *Trachelostyla*, is – like *Gonostomum* – an 18-cirri hypotrich with the postoral ventral cirri displaced anteriad (e.g., Gong et al.

[1] According to molecular data, *Holosticha* as defined by Berger (2006a) branches off outside the core-urostyloids (e.g., Yi et al. 2008, Paiva et al. 2009).

2006). Cell division and molecular data indicate that *Trachelostyla* branches off very early in the Hypotricha tree (Shao et al. 2007, Berger 2008).

Corliss (1961), Borror (1972), and Jankowski (2007) classified it in the Oxytrichidae, a group now characterised mainly by the complex dorsal ciliature, that is, dorsal kinety fragmentation (Berger 1999). Nothing is known about the number (perhaps four because four caudal cirri are present; Fig. 56a) and arrangement of the dorsal kineties; however, I suppose that *T. bryophila* has – like *Wallackia* and *Gonostomum* – only bipolar kineties, that is, lacks kinety fragmentation and dorsomarginal kineties. *Trachelochaeta bryophila* has four very long caudal cirri which are reminiscent of that of *Wallackia* (Fig. 39a, 56a). Of course a detailed redescription is needed to corroborate or disprove this hypothesis.

Hemberger (1982) and Tuffrau & Fleury (1994, p. 141) assigned *Trachelochaeta* to the Amphisiellidae, a taxon recently revised by Berger (2008). However, in this group the right frontoventral row is a mixed row, that is, it is formed from two or more fragments and anlagen, respectively (vs. from one anlage in *Wallackia* which closely resembles the present genus).

Small & Lynn (1985) classified *Trachelochaeta*, together with *Wallackia* and *Gonostomum*, in the Gonostomatidae (Table 3), a classification retained in the present review because of the following features: gonostomatid adoral zone; cirral pattern similar to *Wallackia*, which is pretty sure a gonostomatid.

Shi et al. (1999, p. 150) mentioned *Trachelochaeta* as incertae sedis in the Hypotrichida, that is, they did not assign it to a certain higher taxon within the hypotrichs. By contrast, Lynn & Small (2002) and Lynn (2008) assigned *Trachelochaeta* to the Kahliellidae. However, this group is characterised by the preservation of parental cirri in postdividers, a feature obviously not present in *Trachelochaeta*.

Species included in *Trachelochaeta*: (1) *Trachelochaeta bryophila* Šrámek-Hušek, 1954 (type species). Incertae sedis: (2) *Oxytricha (Opisthotricha) elongata* Grandori & Grandori, 1934.

Species misplaced in *Trachelochaeta*: The following species – largely originally classified in *Trachelochaeta* – are now assigned to other genera within the gonostomatids, or they do not belong to this group at all. If you do not find a certain name in the list below, see the index.

Trachelochaeta bujoreani (Lepsi, 1951) Hemberger, 1982. Remarks: Hemberger (1982, p. 44) synonymised *Wallackia schiffmanni*, type of *Wallackia* (p. 206), with *Paraholosticha bujoreani* and simultaneously transferred it to *Trachelochaeta*. However, *Trachelochaeta bryophila*, type of *Trachelochaeta*, has distinct transverse cirri (vs. very indistinct or lacking in *Wallackia bujoreani*), anteriorly shortened frontoventral rows IV and V (vs. not shortened), and a narrowed anterior body portion (vs. not narrowed). Thus, the classification of *P. bujoreani* in *Trachelochaeta* seems not justified. The synonymy of *Wallackia bujoreani* and *W. schiffmanni*, also proposed by Hemberger (1982), cannot be one hundred per cent excluded.

Trachelochaeta gonostomoida Hemberger, 1985. Remarks: Now *Gonostomum gonostomoidum* (Hemberger, 1985) Berger, 1999 (p. 158). Neither the body shape

nor the cirral pattern of this species are reminiscent of that of *T. bryophila*. The oral apparatus (adoral zone; paroral composed of few, single cilia; endoral distinctly behind paroral) and the cirral pattern (e.g., postoral ventral cirri right of proximal portion of adoral zone) show that it belongs to *Gonostomum* (p. 58).

Trachelochaeta petergoffii Alekperov, 2005. Remarks: This species lacks transverse cirri and the remaining cirral pattern also does not agree with that of *T. bryophila*, type of *Trachelochaeta*. Now classified in *Neowallackia* (p. 298).

Trachelochaeta terrestris Alekperov, 2005. Remarks: The cirral pattern, the gonostomatid oral apparatus, and the nuclear apparatus indicate that this species is closely related to or even synonymous with *Gonostomum gonostomoidum* (Hemberger, 1985) Berger, 1999 (p. 158). I preliminary classify it as valid species of *Gonostomum* (p. 164).

Key to *Trachelochaeta bryophila* and *Oxytricha elongata*

Note that both species mentioned in the following key have not been reliable confirmed, indicating that they are very rare. When you cannot identify your specimen or population with the key below, see also *Wallackia* (p. 206).

1 Anterior body portion narrowed; cirri on frontal area form distinct pairs; postoral area with two cirral rows; four long caudal cirri (Fig. 56a). . . . . *Trachelochaeta bryophila* (p. 303)

- Anterior body portion not narrowed; cirri on frontal area do not form pairs; postoral area blank; three long caudal cirri (Fig. 56c). . . . . *Oxytricha (Opisthotricha) elongata*, incertae sedis in *Trachelochaeta* (p. 306)

Single species

Trachelochaeta bryophila Šrámek-Hušek, 1954
(Fig. 56a, b)

1954 ***Trachelochaeta bryophila* sp. n.** – Šrámek-Hušek, Arch. Protistenk., 100: 265, Abb. 22 (Fig. 56a; original description; no formal diagnosis provided and very likely no type material available).

1972 ***Trachelochaeta bryophila* Šrámek-Hušek, 1954** – Borror, J. Protozool., 19: 15, Fig. 41 (Fig. 56b; revision of hypotrichs).

1974 ***Trachelochaeta bryophila* Šramek-Hušek** – Stiller, Fauna Hung., 115: 88, Fig. 53 (redrawing of Fig. 56a; revision of hypotrichs).

1983 ***Trachelochaeta* Šrámek-Husek, 1954** – Curds, Gates & Roberts, British and other freshwater ciliated protozoa, p. 416, Fig. 245 (redrawing of Fig. 56a; guide to freshwater genera).

1985 ***Trachelochaeta bryophila*** – Small & Lynn, Ciliophora, p. 455 (Fig. 56b; guide to ciliate genera).

2001 ***Trachelochaeta bryophila* Šrámek-Hušek, 1954** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 89 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2002 ***Tracelochaeta bryophila* Srámek-Husek, 1954** – Lynn & Small, Ciliophora, p. 455 (Fig. 56b; guide to ciliate genera; incorrect spelling of *Trachelochaeta*).

Nomenclature: No derivation of the species-group name is given in the original description. The name *bryophil·us, -a, -um* ([m; f; n]; "moss-loving") is a composite of the Greek noun *to bryon* (the moss) and the Greek *philos* (loving) and obviously alludes to the habitat (Bryales-community, a group of mosses) where the species was discovered. Type species of *Trachelochaeta*. *Trachelochaeta sphagni* in Šrámek-Hušek (1954, p. 256; ecology section of *Chilodonella macrostoma*) is obviously an invalid name for the type species because on page 266 Šrámek-Hušek (1954) wrote that *T. bryophila* was discovered at the same locality as *Chilodonella macrostoma* Šrámek-Hušek, 1954 (see also Berger 1999, p. 894; 2001, p. 89). Incorrect original spelling: *Trachelochaeta bryoqhila* (Šrámek-Hušek 1954, p. 265, legend; see also Jankowski 1979, p. 67). Incorrect subsequent spellings: *Trachelochaeta bryophia* (Takahashi & Suhama 1991, p. 106); *Trachelochaeta bryophylla* Sramek-Husek, 1954 (Alekperov 2005, p. 218).

Remarks: *Trachelochaeta bryophila* is described after live observations only. Thus, some details of the infraciliature (e.g., exact arrangement of cirri, variability, dorsal kinety pattern, undulating membranes) are not known. Consequently, a detailed redescription is needed to estimate the phylogenetic position of this obviously rare species. A synonymy of *Trachelochaeta bryophila* and *Wallackia* spp. (e.g., *W. schiffmanni*) is unlikely because of the following differences: body slender and anterior body portion narrowed against shaped like a typical *Gonostomum* species; long frontoventral rows do not extend anteriorly against not shortened anteriorly; five distinct transverse cirri against no or only two indistinct transverse cirri; dorsal bristles likely 10–20 µm against 5–10 µm; three caudal cirri against four. According to the available data, *Trachelochaeta bryophila* is characterised by the following features: curious body shape, that is, anterior portion distinctly narrowed ("cephalised"); cirral pairs (likely pseudo-pairs) in frontal area; long caudal cirri.

Borror (1972) made a schematic redrawing (Fig. 56b) of the original illustration (Fig. 56a). However, he unnecessarily increased the number of cirri in the various rows, for example, from 11 to 17 in the left frontoventral row (row IV in Fig. 56a).

Morphology: Body size 80–110 × 25–35 µm, body length:width ratio of specimen illustrated about 5.1:1 (Fig. 56a). Anterior body portion (about 40% of body length in specimen illustrated) distinctly narrowed, body thus roughly club-shaped or cephalised (Fig. 56a). Two ellipsoidal macronuclear nodules about in midline of central cell portion, distinctly separated from each other (Fig. 56a). Micronuclei not seen. Contractile vacuole near left body margin, close behind proximal end of adoral zone. No cortical granules described. Jerky movement.

Adoral zone occupies 50% of body length (46% in specimen illustrated), gonostomatid, that is, zone commences at anterior end, extends along anterior left body margin, and curves abruptly obliquely rightwards (Fig. 56a). Adoral zone "dense", that is, number of membranelles rather high, cilia of membranelles relatively short.

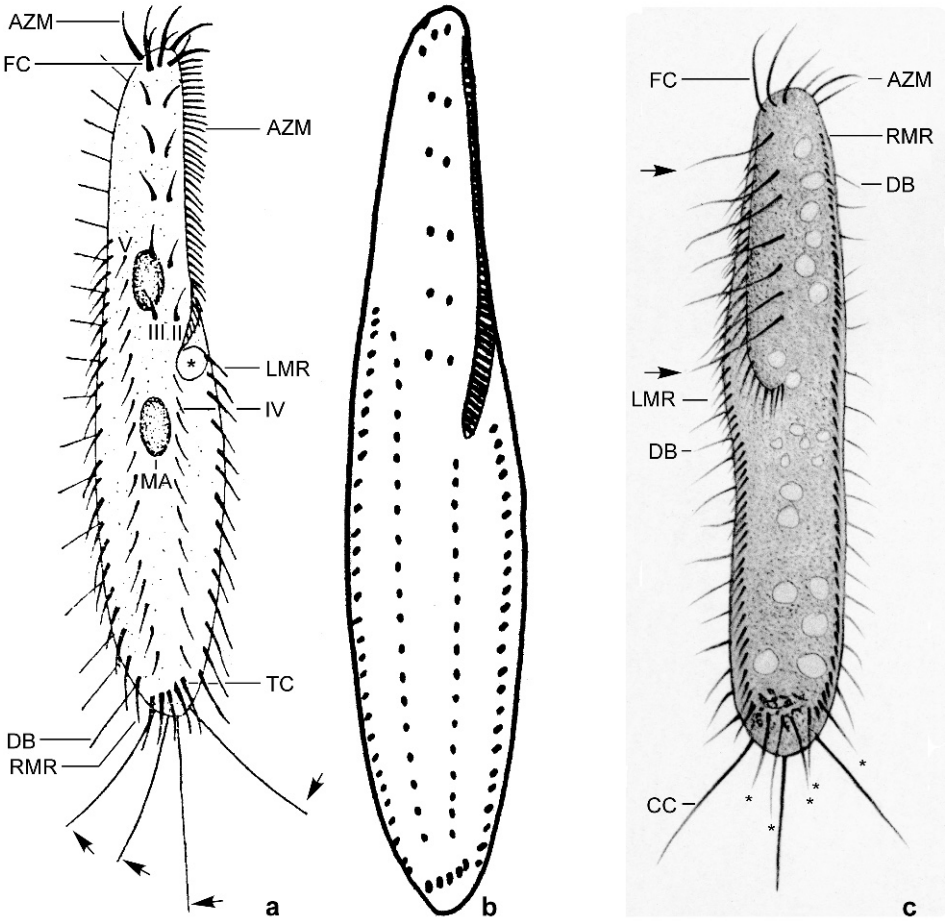

Fig. 56a, b *Trachelochaeta bryophila* (a, from Šrámek-Hušek 1954; b, after Šrámek-Hušek 1954 from Borror 1972. a, b, from life). Ventral view, size not indicated, body length according to text 80–110 µm. Asterisk marks contractile vacuole. Arrows denote the four fine caudal cirri. Page 303.

Fig. 56c *Oxytricha (Opisthotricha) elongata* (from Grandori & Grandori 1934. From life). Infraciliature of ventral side as seen from dorsal, 120 µm. Arrows mark anterior and posterior end of frontoventral row; asterisks mark transverse cirri. Page 306.

AZM = adoral zone of membranelles, CC = caudal cirri, DB = dorsal bristles, FC = right (a) and left (c) frontal cirrus, LMR = left marginal row, MA = rear macronuclear nodule, RMR = right marginal row, TC = transverse cirri, II–V = frontoventral rows (designation has to be confirmed by redescription and ontogenetic data).

Details of oral apparatus not known; buccal field likely very narrow; undulating membranes not described, indicating that they are inconspicuous.

Cirral pattern, although studied from life only, seems reliable (Fig. 56a); in spite of that, details must not be overinterpreted. Three slightly enlarged frontal cirri. Right of adoral zone four or five pairs (likely pseudo-pairs; see Berger 2006a, p. 3)

of slightly enlarged cirri; rows very likely homologous to the frontoventral rows II and III of *Wallackia* (Fig. 39a, 56a). One cirral row (frontoventral row IV?) extends from proximal end of adoral zone to near transverse cirri, in specimen illustrated composed of 11 cirri. Right frontoventral row (frontoventral row V?), like right marginal row, strongly shortened anteriorly (commences about at 29% of body length and composed of 17 cirri in specimen illustrated), terminates near transverse cirri. Distinct pretransverse ventral cirri lacking. Five slightly enlarged transverse cirri (protrude distinctly beyond rear cell end) illustrated, but not mentioned in text (Fig. 56a); possibly, he misinterpreted them as ventral cirri because he wrote "2 closed ventral-rows"; however, the oblique arrangement and the size (distinctly stronger illustrated than the ventral cirri) clearly indicate that these are true transverse cirri. The number – five, as in many hypotrichs which produce their cirri from six (I–VI) anlagen – is difficult to interpret because very likely only five anlagen are present; perhaps one is not a transverse cirrus, but a pretransverse ventral cirrus. Right marginal row distinctly shortened anteriorly (see above), ends – like left row – slightly subterminally; left marginal row commences about at level of buccal vertex.

Dorsal ciliature not known in detail. Bristles long, according to illustration at least about 10 µm, except for rear portion where they are likely up to 20 µm long! At rear cell end four long, fine caudal cirri (Fig. 56a). Number of dorsal kineties not known; provided that each kinety ends with one caudal cirrus as in many other non-dorsomarginalian hypotrichs, then *T. bryophila* has four kineties.

Occurrence and ecology: Very likely a limnetic species and possibly confined to stagnant waters. Type locality of *T. bryophila* is an old moorland near the Vltava river (= River Moldau) south of Cerná, Bohemian Forest, Czech Republic. Šrámek-Hušek (1954, p. 255, 256) found it there in a beta-mesosaprobic Bryales-community of the littoral of a small pond (pH 6.9). The littoral was grown with *Elodea* and Bryales and surrounded by *Carex* sp., *Comarum palustre*, and *Eriophorum vaginatum*. The Bryales-stocks were colonised, inter alia, by *Chilodonella macrostoma*, *Paramecium bursaria*, *Euplotes patella*, *Stylonychia mytilus*, *S. muscorum*, *Paruroleptus piscis*, *Frontonia atra*, *Coleps hirtus*, *Spirostomum filum*, and *Dichilum sphagni* (all names as given by Šrámek-Hušek 1954). Takahashi & Suhama (1991, p. 106; no morphological data) recorded it from a paddy field in Japan. No further records published. Food not known.

Incertae sedis in *Trachelochaeta*

Oxytricha (Opisthotricha) elongata Grandori & Grandori, 1934 (Fig. 56c)

1934 ***Opisthotricha elongata* n. sp.** – Grandori & Grandori, Boll. Lab. Zool. agr. Bachic. R. Ist. sup. agr. Milano, **5**: 290, Tavola XIII, fig. 278 (Fig. 56c; original description; for correct basionym, see nomenclature).

1999 ***Opisthotricha elongata* Grandori & Grandori, 1934** – Berger, Monographiae biol., 78: 242 (brief note, see remarks).

1999 ***Oxytricha (Opisthotricha) elongata* Grandori & Grandori, 1934** – Berger, Monographiae biol., 78: 242 (brief note, see remarks).

2001 ***Oxytricha (Opisthotricha) elongata* Grandori and Grandori, 1934** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 59 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2008 ***Oxytricha (Opisthotricha) elongata* Grandori & Grandori, 1934** – Berger, Monographiae biol., 88: 477 (brief note, see remarks).

Nomenclature: No derivation of the name is given in the original description. The species-group name *elongat·us*, *-a*, *-um* (Latin adjective [m, f, n]; elongated, stretched) obviously refers to the elongate body. Grandori & Grandori (1934, p. 288, 290) classified *Opisthotricha* as subgenus of *Oxytricha*, likely referring to Kahl (1932).[1] Consequently, the correct basionym is *Oxytricha (Opisthotricha) elongata* Grandori & Grandori, 1934 as already stated by Berger (1999), and "*Opisthotricha elongata* Grandori & Grandori, 1934" in Foissner (1998, p. 206) is a combination which formally does not exist. Further, this name is not a primary homonym of *Opisthotricha elongata* Smith, 1897 (for review, see Berger 1999, p. 136), which was, however, transferred to *Oxytricha* by Kahl (1932, p. 609). Thus, at present *Oxytricha elongata* (Smith, 1897) Kahl, 1932 and *Oxytricha elongata* Grandori & Grandori, 1934 are secondary homonyms. In spite of this nomenclatural problem I preliminary do not introduce a replacement name for the younger species because both taxa are rather inexactly described and therefore each generic assignment would be arbitrarily. Thus, the mention of the authorship is mandatory at present.

Remarks: Grandori & Grandori (1934) found only one specimen and therefore could not study this species in detail. They (preliminary?) assigned it to *Oxytricha (Opisthotricha)* Kent, 1882 (p. 785; originally established as genus), a taxon presently usually synonymised with *Oxytricha* (e.g., Borror 1972, p. 14; Berger 1999, p. 115) because the diagnostic feature of *Opisthotricha* (presence of caudal cirri) is also characteristic for *Oxytricha*. Grandori & Grandori (1934) also discussed a relationship with *Gonostomum* because of the gonostomatid oral apparatus, but finally assigned their species to *Oxytricha*. Of course, this newly discovered species was not included in Kahl (1935), and likely for that reason it was overlooked until the end of the century, for example, by Borror (1972). Just Foissner (1998, p. 206) recalled this terrestrial species in his compilation of the world soil ciliates. In the review on oxytrichids I speculated that it very likely belongs to *Trachelostyla* Borror, 1972 or *Trachelochaeta*. However, in the review on *Trachelostyla* I argued that these classifications are also incorrect, because *Trachelostyla* is a group of marine, cephalised (anteriorly narrowed) 18-cirri hypotrichs (for review, see Berger 2008, p. 474), and an inclusion in *Trachelochaeta* seems incorrect because its type species is limnetic and has four cirral rows. The latter statement is still relevant, but because of

[1] Accordingly, we have to assume that the classification of *Urosoma* as genus by Grandori & Grandori (1934, p. 290) is a misprint. Otherwise *Opisthotricha* and *Stylonychia* have to be interpreted as subgenera of *Urosoma* according to the array of the genera and subgenera in Grandori & Grandori (1934).

the similar habitus I preliminary attach *Oxytricha elongata* to *Trachelochaeta*. Of course I do not transfer *O. elongata* to *Trachelochaeta* because such an assignment would be arbitrarily. *Oxytricha elongata* differs from *T. bryophila* (i) in the cirral pattern (paired cirri in frontal area and four cirral rows in middle and rear portion vs. single row in frontal area and two rows on postoral region, supposed that the structures labelled as dorsal bristles in Fig. 56c are indeed dorsal bristles); (ii) the number of caudal cirri (4 vs. 3); and (iii) the shape of the anterior body portion (narrowed vs. not narrowed).

Grandori & Grandori (1934) illustrated the ventral infraciliature as seen from the dorsal side (Fig. 56c). On each side two distinct rows are recognisable, and according to the original description the off-standing structures are the long dorsal bristles, similar to those in *Oxytricha sphagni* Kahl, 1932 (Fig. 59 in Berger 1999). Although the original interpretation of the off-standing structures as dorsal bristles cannot be dismissed as wrong, it cannot be excluded that these structures are cirral rows.

The gonostomatid oral apparatus and the conspicuous caudal cirri of *O. elongata* are highly reminiscent of *Wallackia* (p. 206). However, in these species the ventral side is covered by cirral rows whereas this part of the cell is blank in the present species. Further, *Oxytricha elongata* has five distinct, clearly setoff transverse cirri, which are lacking in *Wallackia*.

A transfer of *O. elongata* to *Gonostomum* also seems not wise at the present state of knowledge because of the very long caudal cirri. Without detailed redescription it is obviously impossible to allocate this highly interesting species to one of the genera previously discussed. Of course one also cannot exclude that it has to be assigned to a not yet described genus, or that the authors made serious misobservations so that it will be unrecognisable for ever.

Morphology: As already mentioned, the description is based on a single specimen (Fig. 56c) and therefore nothing is known about the variability. Body length 120 µm in life; length:width ratio 5:1, that is, body width about 24 µm. Body outline elongate, both ends broadly rounded, right margin straight, left one more or less distinctly vaulted at level of buccal vertex. Consistency of body, nuclear apparatus, contractile vacuole, presence/absence of cortical granules, and movement not described. Cytoplasm with many vacuoles. Adoral zone gonostomatid, occupies 45% of body length, according to text more than 50% long; no further details (e.g., undulating membranes) of oral apparatus known. Three frontal cirri. Seven obviously very long cirri form conspicuous row along adoral zone. No further frontoventral or postoral cirri on ventral side; however, it cannot be excluded that Grandori & Grandori (1934) overlooked them. Five transverse cirri slightly projecting beyond rear end of cell. One left and one right marginal row. According to Grandori & Grandori (1934), the off-standing structures are likely dorsal bristles, similar to those of *Oxytricha sphagni* (Fig. 59 in Berger 1999); presumed that the cell illustrated is 120 µm long, the bristles are at least up to 8 µm long; however, the structures are rather strong so that one cannot exclude that these are cirri. Three very conspicuous and widely separated caudal cirri; about 27 µm long according to Fig. 56c. Number and arrangement of dorsal kineties not known.

Occurrence and ecology: So far only recorded from the type locality, that is, San Donato Milanese (45°25'N 9°16'E), a municipality near the city of Milan, Northern Italy. Grandori & Grandori (1934) discovered this species in soil (pH = 7.2) from agriculturally used grassland which was flooded with water from a sewer (details see Grandori & Grandori 1934, p. 61, "Terreno III"). No further records published. Food not known.

Circinella Foissner, 1994

1994 ***Circinella* nov. gen.**[1] – Foissner, Europ. J. Protistol., 30: 157 (original description). Type (by original designation): *Circinella arenicola* Foissner, 1994.
1999 ***Circinella* Foissner, 1994** – Shi, Acta Zootax. sinica, 24: 253 (generic revision of hypotrichs).
1999 ***Circinella* Foissner, 1994** – Shi, Song & Shi, Progress in Protozoology, p. 100 (generic revision of hypotrichs).
2001 ***Circinella* Foissner 1994** – Aescht, Denisia, 1: 42 (catalogue of generic names of ciliates; see nomenclature).
2001 ***Circinella* Foissner, 1994** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 15 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Circinella* Foissner, 1994** [2] – Lynn & Small, Phylum Ciliophora, p. 451 (guide to ciliate genera; see nomenclature).
2007 ***Circinella* Foissner, 1994** – Jankowski, Phylum Ciliophora, p. 459 (generic revision of ciliates).
2008 ***Circinella* Foissner, 1994** – Lynn, Ciliated protozoa, p. 357 (revision of ciliate families).
2008 ***Circinella* Foissner, 1994** – Berger, Monographiae biol., 88: 467 (brief note on exclusion of genus from the amphisiellids).

Nomenclature: The Latin word "*circinella*" means tiny, curled hair, obviously alluding to the more or less distinctly spiralled general appearance of the type species (Foissner 1994a). Feminine gender (Foissner 1994a).

Characterisation (A = supposed apomorphy): Filiform hypotrichs (Gonostomatidae?) with very short (less than 10% of body length!), bipartite adoral zone of membranelles (A?). Three inconspicuous frontal cirri, usually one buccal cirrus, and one or more parabuccal cirri. Frontoventral row extends beyond level of adoral zone of membranelles. One right and one left marginal row. Frontoterminal cirri, postoral ventral cirri, pretransverse ventral cirri, and transverse cirri lacking. Three (*C. arenicola*, *C. vettersi*) or one (*C. filiformis*) dorsal kineties. Opisthe's oral apparatus and frontoventral ciliature and proter's frontoventral row originate and develop without participation of parental cirri (A?). Frontoventral ciliature originates from four anlagen only, including the frontoventral row, which is formed from a single anlage. Caudal cirri, dorsomarginal kinety, and dorsal kinety fragmentation lacking. Terrestrial.

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[1] Foissner (1994a) provided the following diagnosis: Filiform Cladotrichidae (?) with short, oblique row of ventral cirri longer than adoral zone of membranelles. 1 left and 1 right marginal row. No transverse and caudal cirri. The opisthe's oral apparatus and frontoventral ciliature and the proter's ventral row originate and develop without participation of parental cirri.

[2] Lynn & Small (2002) provided the following characterisation: Elongate, worm-like body with slightly enlarged anterior end; transverse cirri, absent; caudal cirri, absent.

Table 21 Morphometric data on *Circinella arenicola* (are, from Foissner 1994a), *Circinella filiformis* (fil, from Foissner 1982), and *Circinella vettersi* (vet, from Berger & Foissner 1989a)

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	are	331.3	330.0	85.1	13.1	25.7	180.0	540.0	42
	fil	108.7	106.0	16.1	5.1	14.9	83.0	140.0	10
	vet	143.6	145.0	18.6	5.2	13.0	112.0	180.0	13
Dividing cells, length	are	171.6	160.0	34.1	7.5	19.9	124.0	245.0	21
Body, width	are	19.6	20.0	2.7	0.4	13.7	15.0	24.0	42
	fil	7.2	6.8	1.3	0.4	18.1	5.0	11.0	10
	vet	12.0	11.0	1.5	0.4	12.7	10.0	15.0	13
Dividing cells, width	are	50.0	50.0	8.2	1.8	16.3	30.0	65.0	21
Adoral zone of membranelles, length	are	24.6	25.0	2.3	0.6	9.4	21.0	30.0	17
	fil	7.8	8.0	0.6	0.2	8.0	6.0	9.0	10
	vet	8.5	8.0	0.9	0.2	10.4	7.0	10.0	13
Anterior body end to rear end of frontoventral row, distance	are	76.1	70.0	17.6	4.3	23.1	50.0	107.0	17
	fil	16.2	16.0	2.3	0.7	14.3	13.0	20.0	10
	vet	16.5	16.0	1.7	0.4	10.1	14.0	20.0	13
Macronuclear nodule, length [b]	are	7.2	7.0	2.1	0.5	28.7	4.0	11.0	17
	fil	5.8	5.3	1.1	0.3	18.6	4.0	8.0	10
	vet	9.2	7.0	4.9	1.4	54.0	3.0	22.0	13
Macronuclear nodule, width [b]	are	3.0	3.0	1.7	0.4	55.4	2.0	9.0	17
	fil	1.9	1.7	0.5	0.2	26.6	1.4	2.6	10
	vet	1.8	1.7	0.4	0.1	21.0	1.2	2.5	13
Macronuclear nodules, number	are	77.8	78.0	14.5	3.6	18.8	46.0	102.0	17
	fil	16.4	15.5	4.6	1.5	28.4	11.0	26.0	10
	vet	27.5	27.0	7.5	2.1	27.2	20.0	50.0	13
Micronucleus, length [b]	are	7.8	8.0	1.7	0.4	21.4	6.0	13.0	17
	fil	1.6	1.5	0.2	0.1	12.8	1.4	1.9	10
	vet	8.2	8.0	1.3	0.4	15.7	7.0	11.0	13
Micronucleus, width [b]	are	2.5	2.5	0.5	0.1	18.9	2.0	3.0	17
	fil	1.6	1.5	0.2	0.1	12.8	1.4	1.9	10
	vet	2.0	2.0	0.5	0.1	24.4	1.4	2.8	13
Micronuclei, number	are	4.9	4.0	1.7	0.4	33.8	2.0	8.0	17
	fil	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
	vet	1.9	2.0	0.5	0.1	25.7	1.0	3.0	13
Adoral membranelles, total number	are	19.9	19.0	2.9	0.7	14.4	15.0	27.0	17
	fil	9.8	10.0	0.9	0.3	8.9	9.0	12.0	10
	vet	8.3	8.0	0.6	0.2	7.6	7.0	9.0	13
Adoral membranelles, number in distal portion	are	7.2	7.0	1.6	0.4	21.5	5.0	12.0	17
Adoral membranelles, number in proximal portion	are	12.8	13.0	1.8	0.4	13.7	9.0	16.0	17
Frontal cirri, number	are	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	fil [c]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	vet	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Buccal cirri, number	are	1.1	1.0	–	–	–	1.0	2.0	17
	fil	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
	vet	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Parabuccal cirri, number	are	1.6	1.0	–	–	–	1.0	5.0	17
	fil [c]	0.0	0.0	–	–	–	0.0	0.0	10
	vet	0.0	0.0	–	–	–	0.0	0.0	13
Frontoventral row, number of cirri	are	25.2	24.0	5.8	1.4	23.0	18.0	37.0	17

Table 21 Continued

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Frontoventral row, number of cirri	fil	8.2	8.0	1.2	0.4	15.2	6.0	10.0	10
	vet	8.2	8.0	1.4	0.4	17.2	6.0	11.0	13
Right marginal row, number of cirri	are	92.8	90.0	17.1	4.2	18.4	71.0	130.0	17
	fil	52.9	50.0	8.8	2.8	16.6	44.0	74.0	10
	vet	68.8	70.0	6.2	1.7	9.0	58.0	78.0	13
Left marginal row, number of cirri	are	102.8	95.0	19.2	4.7	18.7	84.0	156.0	17
	fil	40.8	39.0	6.7	2.1	16.4	33.0	55.0	10
	vet	52.1	53.0	4.7	1.3	9.1	43.0	60.0	13
Dorsal kineties, number	are	3.4	3.0	–	–	–	3.0	4.0	17
	fil	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
	vet	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] In *C. vettersi* the rearmost macronuclear nodule/micronucleus was measured; in the other two species no specification was made.

[c] The cirrus behind the right frontal cirrus is included in the number of frontal cirri, but it cannot be excluded that *C. filiformis* has only two frontal cirri (left and right one or middle and right one) and one parabuccal cirrus (= cirrus III/3; see text for details).

Additional characters: Slender specimens (previously termed theronts) and thicker, well-nourished, sluggish specimens (previously termed trophonts) present. Body flexible, almost circular in cross-section, except for anterior body portion. More than eight macronuclear nodules. Two or more contractile vacuoles. Cortical granules lacking. Movement slow, roughly nematoda-like. Undulating membranes inconspicuous and buccal field very narrow due to very short adoral zone. All cirri very fine. Marginal cirri relatively narrowly spaced. Dorsal bristles short (2–4 µm), relatively widely spaced. Feed likely mainly on bacteria. Form resting cysts (because terrestrial).

Remarks: *Circinella* species are rather conspicuous because they are filiform and of middle or large size. Thus, they resemble nematodes and it cannot be excluded that they have been confused with this metazoan group at superficial observations previously.

Circinella arenicola and congeners have, of course, a very similar, relatively simple infraciliature composed of only two marginal rows, three small frontal cirri, an inconspicuous buccal cirrus, one or more parabuccal cirri, and a frontoventral row extending more or less distinctly beyond the level of the buccal vertex and originating from a single anlage according to the ontogenetic data on the type species (Foissner 1994a; Fig. 59o–v). Many parts of the ordinary ciliature of a hypotrich (frontoterminal cirri, postoral ventral cirri, pretransverse ventral cirri, transverse cirri, caudal cirri) are lacking. Whether the cirri at the rear cell end of *C. filiformis* and *C. vettersi* are marginal, transverse, and/or caudal cirri is unclear because

the cirral pattern of this region is very difficult to analyse and interpret correctly without ontogenetic data.

Circinella has only four frontoventral cirri anlagen (Fig. 59j–n). Since the last common ancestor of the hypotrichs had very likely six anlagen (Berger 2006a, p. 33; 2008, p. 23), we have to assume that two anlagen get lost during the evolution of *Circinella*. Although the frontal cirri of *Circinella* are rather small, that is, not distinctly larger than the remaining cirri as this is the case in most other hypotrichs, we can conclude from their position behind the distal portion of the adoral zone and the ontogenetic pattern in the type species that they originate, as is usual, from the anlagen I–III. By contrast, it is more speculative to find out with which anlage, respectively, part of the ciliature of an 18-cirri hypotrich the frontoventral row of *Circinella* is homologous. In *C. arenicola* the parental frontoventral row is obviously not involved in primordia formation (Fig. 59f, i). Such a non-participation in anlagen formation is characteristic for the frontoterminal cirri originating from anlage VI (= cirri VI/3 and VI/4 in 18-cirri hypotrichs [e.g., Fig. 7a in Berger 2008]; Fig. 23 in Berger 1999) or the cirral row formed by anlage VI in *Pseudouroleptus*, a somewhat unusual oxytrichids (for reviews, see Berger 1999, p. 888; 2008, p. 658). Consequently, one can conclude that anlagen IV and V have been lost in *Circinella*; however, this assumption is only a first basis for discussion. The oral primordium of *C. arenicola* originates about in mid-body, that is, at a site where the oral primordium of many hypotrichs occurs. Since there are no parental cirri it originates de novo, perhaps a further apomorphy of *Circinella*.

Circinella species obviously have the smallest oral apparatus within the hypotrichs (8% of body length in type species; 6% in *C. vettersi*; 7% in *C. filiformis*), mainly because the number of adoral membranelles is rather low (20 in the very long type species, below 10 in the congeners). Perhaps the small size of the oral apparatus is, together with the very slender body shape, a perfect adaptation to the terrestrial modus vivendi. Due to the small size of the zone, the undulating membranes and the buccal area are also very small and thus difficult to analyse. Probably, electron microscopical methods, or at least perfect protargol preparations are needed to study these fine structures in detail. Interestingly, the adoral zone of *Circinella* is not only very small, but also distinctly bipartite (Fig. 57c, o, s, 60g, 61g, i). However, a more or less conspicuous gap in the adoral zone is also known from several other genera, for example, the urostyloid *Uroleptopsis* Kahl, 1932 (Berger 2004; for review, see Berger 2006a, p. 980), *Vermioxytricha* (for review, see Berger 2008, p. 596), and *Erniella* Foissner, 1987d, a genus of uncertain systematic position. This distribution clearly shows, that a distinct gap in the adoral zone evolved several times independently.

Foissner (1994a) classified *Circinella* provisionally in the Cladotrichidae Small & Lynn, 1985 because of the apokinetal origin and development of the oral apparatus and ciliature of the opisthe and the lack of frontoterminal, midventral, transverse, and caudal cirri, a combination of features basically matching the very vague diagnosis of the cladotrichids: “Frontal file, on right, rarely extends past mid-body; at

least 1 left and 1 right marginal files". He also discussed that a classification in the amphisiellids is inappropriate because of ontogenetic differences (Eigner & Foissner 1994). In the amphisiellids the median cirral row is composed of cirri originating from the two or three rightmost anlagen. In addition, the oral primordium originates in very close contact to the parental amphisiellid median cirral row (Berger 2004a, 2008). By contrast, the frontoventral row of *Circinella arenicola* originates from a single anlage and the oral primordium is unambiguously formed de novo (Fig. 59a, j–n). In spite of these evident differences, Shi (1999), Shi et al. (1999), Lynn & Small (2002), and Jankowski (2007) classified *Circinella* in the Amphisiellidae. Lynn (2008) was somewhat uncertain and therefore put it as incertae sedis in the amphisiellids. Although Foissner (1994a) knew about the differences in the participation of the frontoventral row(s) (yes in *Cladotricha* vs. no in present genus), he refrained from the establishment of a monotypic, and therefore redundant family. I basically follow Foissner (1994a) and classify *Circinella* in the same higher taxon as *Cladotricha*. However, since Lynn & Small (2002) have submerged the cladotrichids in the kahliellids, I put *Circinella* in the gonostomatids, to which I assign *Cladotricha* (p. 235). Of course, the classification of *Circinella* as incertae sedis in the gonostomatids is only preliminary because of the lack of a good agreement; the presence of two marginal rows and a more or less long frontoventral row is of course rather meagre.

Eigner (1997, p. 558) removed *Circinella* from the Cladotrichidae and put it into the Orthoamphisiellidae. According to the diagnosis of the orthoamphisiellids provided by himself, "the two rightmost ventral rows develop each by one within anlage." However, in *Circinella* neither the parental frontoventral row is involved in the anlagen formation of the new frontoventral rows nor do the frontoventral rows of proter and opisthe originate from a common anlage, that is, a primary primordium. Thus, Eigner's decision is inexplicable, and perhaps for that discrepancy Eigner (1997) himself wrote that the assignment to the orthoamphisiellids is only provisionally, but better than any other classification.

In the following paragraphs, *Circinella* is compared with some similar genera. However, the differences discussed indicate that the similarity is mainly based on plesiomorphies and/or convergencies.

Engelmanniella Foissner, 1982 resembles *Circinella* in body shape, size, nuclear apparatus, and cirral pattern. However, in *Engelmanniella mobilis*, the sole species, parental and grandparental marginal cirri are retained which is reminiscent of the kahliellids. Thus, *Engelmanniella* is preliminary assigned to this group (p. 498). *Engelmanniella* and *Circinella* agree also in the de novo formation of a dorsal kinety. However, these de novo-formed kineties are likely not homologous (dorsal kinety 1 in *C. arenicola* vs. kinety 2, respectively rightmost kinety of opisthe only in *E. mobilis*), indicating that the agreement is only a convergence (see also Eigner 1997). In addition, the frontoventral rows are differently formed, namely by two within anlagen (one for the proter, one for the opisthe) in the parental row in *Engelmanniella*

mobilis[1] against from a branch of opisthe's oral primordium in *C. arenicola*. These differences indicate that *Engelmanniella* and *Circinella* are not closely related. Of course, relevant molecular data are needed to support or disprove this hypothesis.

Circinella also shows some resemblance to *Hemisincirra* Hemberger, 1985, a group of slender, terrestrial species which have a (often irregular) frontoventral row which is either slightly shorter, as long as, or slightly longer than the adoral zone (for review, see Berger 2008, p. 387). Unfortunately, for the type species *H. buitkampi* (Jankowski, 1979) some important features (e.g., presence/absence of frontoterminal cirri; formation of frontoventral row) are not known (Fig. 77a–c in Berger 2008). Berger (2008) supposed that the frontoventral row originates from two or three anlagen because the cirri are arranged in a zigzag-pattern. For that reason and because transverse cirri are present, a close relationship of *Circinella* and *Hemisincirra* is unlikely. *Hemisincirra* has been revised recently, and although many species have been transferred to other genera earlier, it is very likely still non-monophyletic (Berger 2008, p. 389). Inter alia for that reason, it has been preliminary classified as incertae sedis in the amphisiellids by Berger (2008). However, three species (*H. rariseta*, *H. vermicularis*, *H. interrupta*) are very similar to the *Circinella* species and therefore they have been included in the key below.

The ventral and dorsal infraciliature of *Paramphisiella* Foissner, 1988, a typical amphisiellid, is also very similar to that of *Circinella* (for review, see Berger 2008, p. 351). However, the frontoventral row, which is distinctly longer, is composed of cirri originating from two anlagen (vs. one in *Circinella*), the relative length of the continuous (vs. bipartite) adoral zone is larger (14–25% vs. below 10%), and caudal cirri are present (vs. lacking).

Vermioxytricha Foissner et al., 2002a, a non-oxytrichid Dorsomarginalia according to Berger (2008, p. 596), comprises two species (*V. arenicola*, *V. muelleri*), which also show some resemblance to *Circinella* species, especially in habitat (soil), body size, body shape, nuclear apparatus, and gap in adoral zone. However, their frontoventral ciliature, which originates from five anlagen (vs. four in *Circinella*), does not extend beyond the buccal vertex, and one dorsal kinety is a dorsomarginal row. Thus, a close relationship of *Vermioxytricha* and *Circinella* is very unlikely.

In the original descriptions of the *Circinella* species the terms theront and trophont have been used for the designation of slender and well-nourished, somewhat broadened specimens, respectively (Foissner 1982, Berger & Foissner 1989a). However, this terminology is not quite correct because, according to Corliss (1979) and Lynn (2008), a theront is basically the dispersal stage in the polymorphic life cycle of parasitic or histophagous ciliates (e.g., ophryoglenine hymenostomes). Essentially it is a more or less transformed tomite (= a small, free-swimming and non-feeding form derived by one or more fissions of a prefission or dividing stage [= tomont]). By contrast, a trophont is defined as mature, vegetative, adult form as an interfissional or feeding or growing stage in the life cycle of any ciliate. Most often, how-

[1] Whether the frontoventral row of *Engelmanniella mobilis* is a true frontoventral row or the inner right marginal row is not quite certain (see p. 502).

ever, a trophont is a specific stage between tomite (or theront) and tomont in the polymorphic life cycle of parasitic or histophagous species. Since *Circinella* species are (very likely) neither parasitic nor histophagous I do not use the terms theront and trophont and replace them by "slender specimens" (for theront) and "well-nourished or well-fed specimens" (for trophont).

Species included in *Circinella* (alphabetically arranged basionyms are given): (1) *Circinella arenicola* Foissner, 1994a (type species); (2) *Hemisincirra vettersi* Berger & Foissner, 1989a; (3) *Perisincirra filiformis* Foissner, 1982.

Key to *Circinella* and similar *Hemisincirra* species

The identification of *Circinella* species is a difficult task requiring some sophisticated features, for example, number of adoral membranelles, dorsal kineties, and macronuclear nodules. Thus, protargol impregnation is needed. The key below is a slightly modified version of Foissner's (1994a) key. Numbers are averages from at least 10 protargol-impregnated specimens. As supplement, the three most similar *Hemisincirra* species are included because they are almost indistinguishable from *Circinella* in life. For further vermiform hypotrichs see, inter alia, *Hemisincirra* (Berger 2008, p. 387), *Vermioxytricha* (Berger 2008, p. 596), and *Engelmanniella mobilis* (p. 498).

1 Frontoventral row distinctly longer than adoral zone (e.g., Fig. 57a, o, 60e, g, 61g, i). . . . . **2** (*Circinella*)
- Frontoventral row as long as adoral zone or shorter (Fig. 86b, 87c, 88a in Berger 2008). **4**

2 Length in life more than 250 µm; anterior body end broadened head-like; 18 adoral membranelles and 24 cirri in frontoventral row; about 78 (46–102) macronuclear nodules distributed throughout cell (Fig. 57a–v). . . . . *Circinella arenicola* (p. 317)
- Length in life 250 µm or less; anterior body end slightly tapered; 10 or less adoral membranelles; about 8 (6–11) cirri in ventral row; 16–27 (11–50) macronuclear nodules (Fig. 60a, 61a). **3**

3 Length in life 150–250 µm; 10 adoral membranelles; macronucleus moniliform, composed of 16 nodules on average; 1 dorsal kinety (Fig. 61a–l). . . . . *Circinella filiformis* (p. 333)
- Length in life about 150 µm; 8 adoral membranelles; on average 27 macronuclear nodules distributed throughout cell; 3 dorsal kineties (Fig. 60a–h). . . . . *Circinella vettersi* (p. 327)

4 (1) Two dorsal kineties (Fig. 86c in Berger 2008). . . . . *Hemisincirra rariseta* (Berger 2008, p. 428)
- One dorsal kinety. **5**

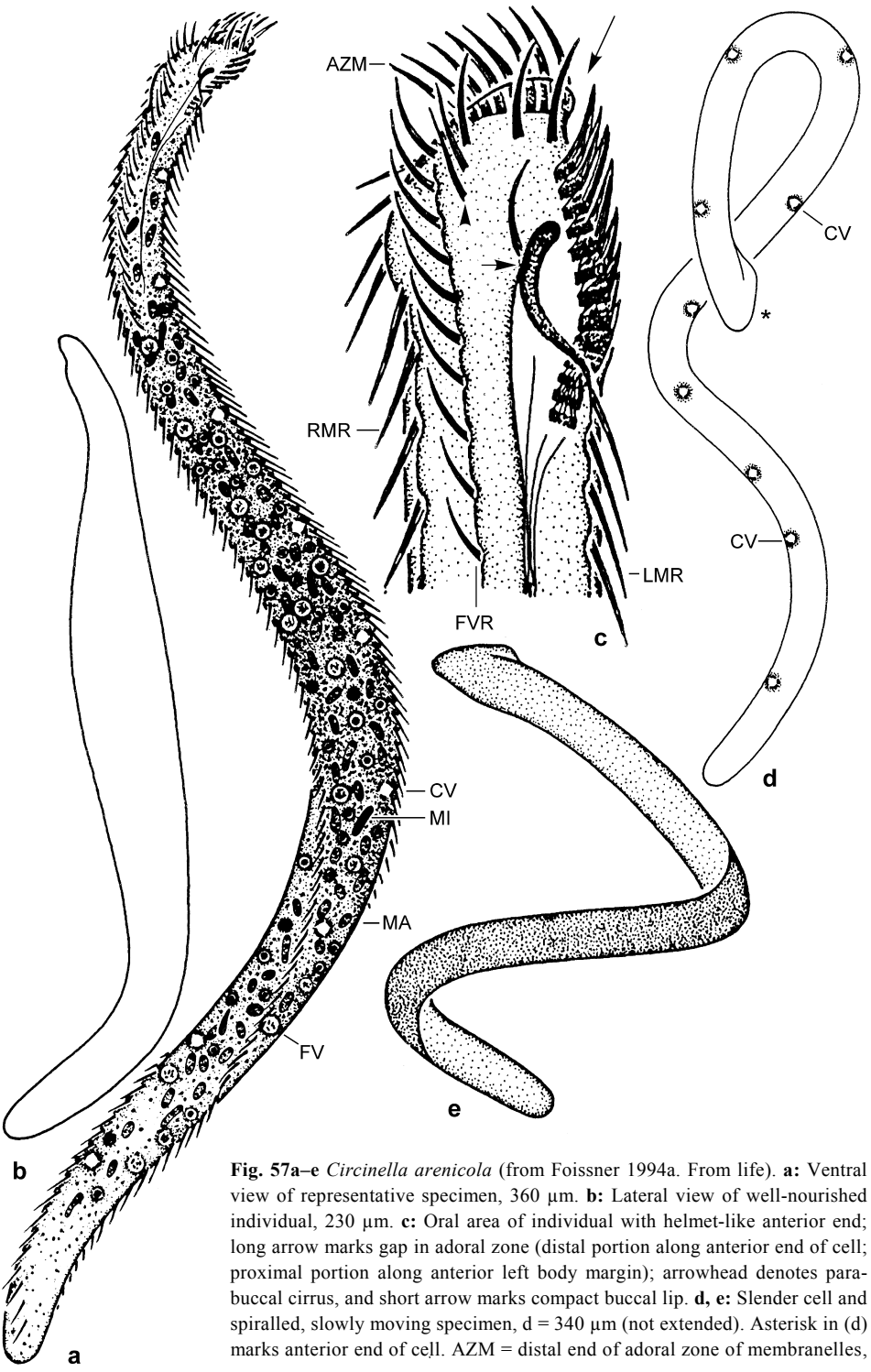


Fig. 57a–e *Circinella arenicola* (from Foissner 1994a. From life). **a:** Ventral view of representative specimen, 360 µm. **b:** Lateral view of well-nourished individual, 230 µm. **c:** Oral area of individual with helmet-like anterior end; long arrow marks gap in adoral zone (distal portion along anterior end of cell; proximal portion along anterior left body margin); arrowhead denotes parabuccal cirrus, and short arrow marks compact buccal lip. **d, e:** Slender cell and spiralled, slowly moving specimen, d = 340 µm (not extended). Asterisk in (d) marks anterior end of cell. AZM = distal end of adoral zone of membranelles,

5 On average about 30 macronuclear nodules; one contractile vacuole (Fig. 87b in Berger 2008). . . . . *Hemisincirra interrupta* (Berger 2008, p. 432)
- On average about 10 macronuclear nodules; four contractile vacuoles (Fig. 88a in Berger 2008). . . . . *Hemisincirra vermicularis* (Berger 2008, p. 435)

Circinella arenicola Foissner, 1994
(Fig. 57a–v, 58a–e, 59a–q, Table 21)

1994 ***Circinella arenicola* nov. spec.**[1] – Foissner, Europ. J. Protistol., 30: 157, Fig. 1–49, Table 1 (Fig. 57a–v, 58a–e, 59a–q; original description; the holotype slide [accession number 1997/23] and a paratype slide [1997/24–27] have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; see also Aescht 2003, p. 380; 2008, p. 143).
1994 ***Circinella arenicola*** – Foissner, Kataloge des O. Ö. Landesmuseums Linz, 71: 170, Abb. 7, 8, 118h (Fig. 57a, g; review about soil protozoa).
1994 ***Circinella arenicola*** – Foissner, Extremophile, p. 206, Abb. 10.4h, 10.7 (Fig. 57a, h, j, k; brief review about protists in extreme biotops).
1997 ***Circinella arenicola* Foissner, 1994** – Eigner, J. Euk. Microbiol., 44: 558, Fig. 12 (redrawing of Fig. 57s, u; schematic representation of cell division).
1999 ***Circinella arenicola*** – Foissner, Agriculture, Ecosystem & Environments, 74: 99, Fig. 6 (Fig. 57h; review on soil protozoa).
2001 ***Circinella arenicola* Foissner, 1994** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 15 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Circinella arenicola*** – Lynn & Small, Phylum Ciliophora, p. 451, Fig. 32 (Fig. 57o, p; guide to ciliate genera; incorrect subsequent spelling).
2006 ***Circinella arenicola*** – Foissner, Acta Protozool., 45: 125, Fig. 17 (Fig. 57g; review about biogeography of micro-organisms).
2007 ***Circinella arenicola* Foissner, 1994** – Jankowski, Phylum Ciliophora, p. 459 (generic revision of ciliates).

Nomenclature: The species-group name *arenicola* (Latin adjective; living in sand) refers to the habitat (sand dunes) where the species was discovered (Foissner 1994a). Foissner (1994a) stated that the holotype slide and a paratype slide have been deposited in Linz. Finally, however, he deposited the holotype and four paratype slides (Aescht 2003, 2008; accession numbers, see first entry in list of synonyms). Type species of *Circinella* Foissner, 1994a.

Remarks: The type species differs from the congeners by the body size, the broadened anterior end, and the high number of macronuclear nodules and contrac-

← CV = contractile vacuole, FV = food vacuole, FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row. Page 317.

[1] Foissner (1994a) provided the following diagnosis: Size *in vivo* about 400 × 22 µm. Filiform, anterior end (oral area) slightly broadened (cephalized). 78 macronuclear nodules on average, distributed throughout cell. Adoral zone of membranelles about 8% of body length, bipartite, on average 7 membranelles in distal and 13 in proximal portion. Right and left row of marginal cirri composed of an average of 90 and 95 cirri, respectively. Ventral row about 21% of body length, consists of 24 cirri on average. Usually 1 buccal cirrus and 3 dorsal kineties.

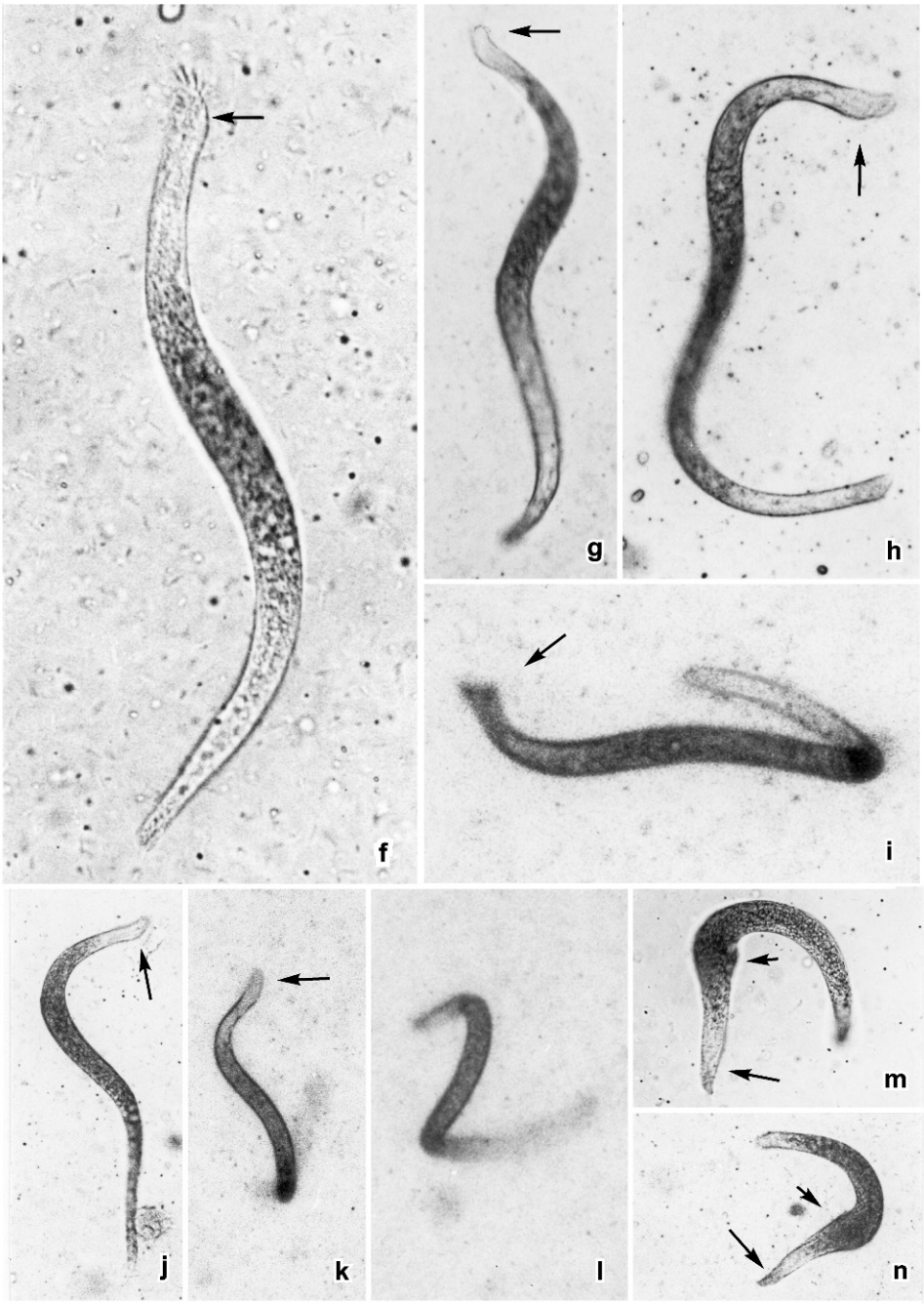


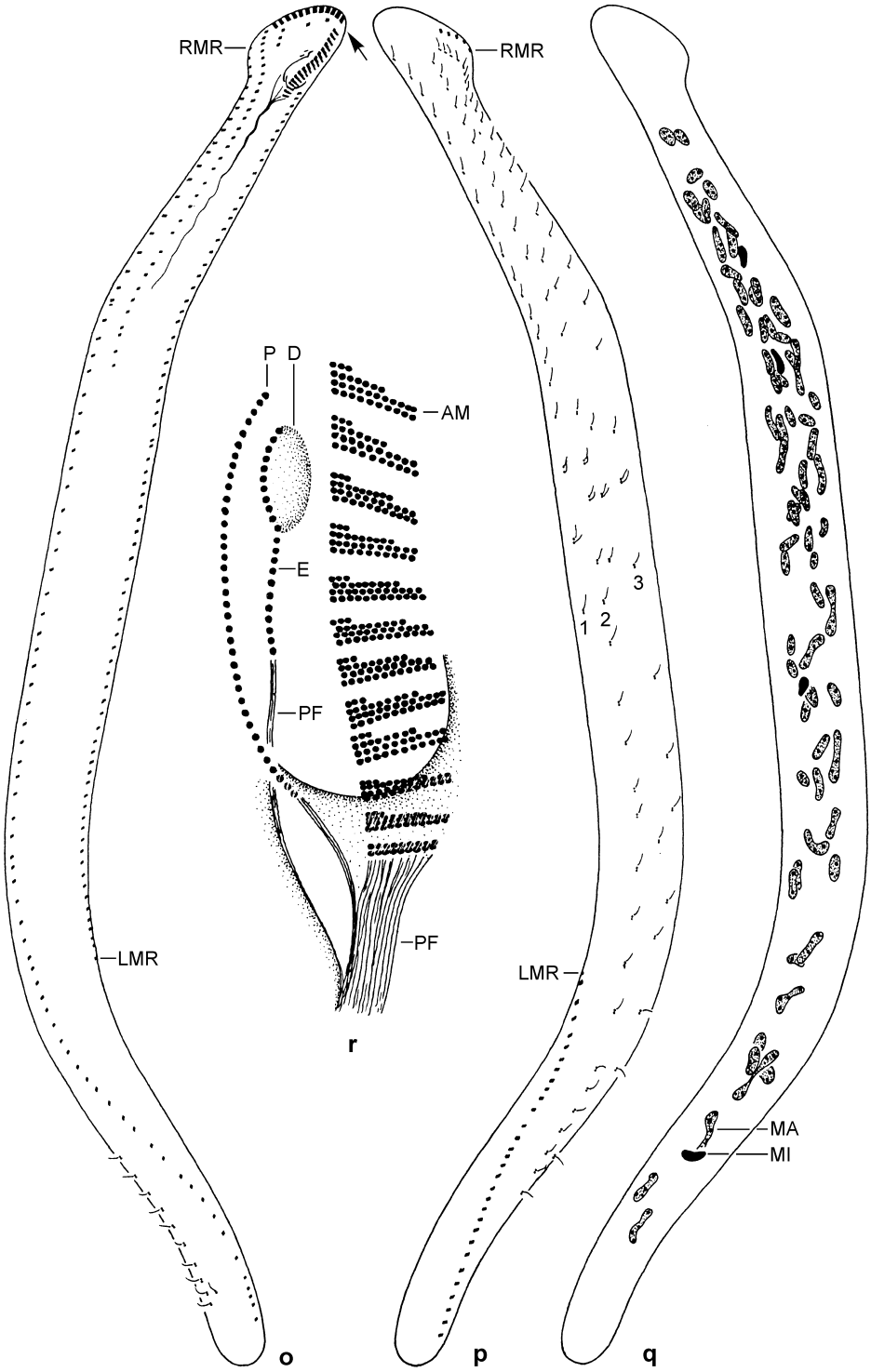
Fig. 57f–n *Circinella arenicola* (from Foissner 1994a. Bright field photomicrographs). **f–l:** Freely moving, typical specimens showing, inter alia, the widened (cephalised) anterior end (arrows). The middle cell portion is packed with food vacuoles and thus dark at low magnification. **m, n:** Specimens with bulbous widening (short arrow). The long arrow denotes the flattened anterior end. Page 317.

tile vacuoles (for details, see key). At superficial observations it resembles *Protospathidium vermiforme* Foissner et al., 2002a, which, however, is, inter alia, smaller and has the contractile vacuole in the rear cell end (for review, see Foissner & Xu 2007, p. 116). In addition, *C. arenicola* is perhaps confined to sand dunes of North America, as indicated by the sole record from the type locality. Thus, records from outside this area have to be confirmed by detailed morphological data.

Morphology: The following review is exclusively based on the very detailed original description, which contains some further photomicrographs of protargol-impregnated specimens documenting the cirral pattern (Foissner 1994a).

Body size, especially length, highly variable, possibly due to injury. In life 200–600 × 18–30 µm, usually around 400 × 22 µm; body length:width ratio thus about 18:1 in life, and about 17:1 on average in protargol preparations (Table 21). Body shape distinct, namely very slender and anterior portion slightly to distinctly broadened (cephalised), so that cells are sometimes reminiscent of very slender spathidiids (Fig. 57a, d–l). Middle third of cell slightly widened, especially in well-nourished individuals, anterior third less attenuated than posterior third and broadened in oral ("head") region. Posterior end rounded. Oral region flattened dorsoventrally about 2:1, postoral area more or less circular in cross-section. About 10% of the individuals have a bulbous dilatation in the anterior body half (Fig. 57m, n); usually this widening is filled with food vacuoles; the infraciliature and nuclear apparatus look, however, normal. Body very flexible, slightly spiralled longitudinally and always more or less distinctly serpentine and coiled (e.g., Fig. 57d, e, l). On average 78 macronuclear nodules distributed throughout cell, ellipsoidal. Micronuclei on average somewhat larger than macronuclear nodules, compact, usually comma-shape, rarely ellipsoidal (Fig. 57a, q, 58a). About 10 contractile vacuoles evenly distributed along left body margin (Fig. 57a, d). Pellicle and cytoplasm colourless, no special cortical granules or cytoplasmic crystals. Middle third of well-fed specimens packed with 3–4 µm-sized food vacuoles and 0.2–2.0 µm-sized silvery shining globules making cells dark at low magnification; anterior and posterior portion usually translucent because of lacking or only few food vacuoles. Movement slow, sluggishly winding, rarely gliding (Fig. 57d–n); cells concentrated in a small drop of water look like a miniaturised worm community.

Oral apparatus occupies only about 8% of body length, that is, very small compared to cell size (Fig. 57a, c, f, o, r, s, 58a–d). Adoral zone bipartite by more or less distinct gap; distal portion composed of about seven membranelles, extends backwards on oblique anterior end; proximal portion composed on average of 13 membranelles and thus somewhat larger than distal one (Table 21). Proximal portion of adoral zone roughly gonostomatid (Fig. 57c, o). Bases of largest membranelles about 5 µm wide, of ordinary structure, that is, composed of four kineties of different length. Buccal cavity narrow but deep, right margin with distinct, compact lip (Fig. 57c). Paroral slightly curved, presumably composed of single row of basal bodies bearing 6 µm long cilia. Endoral also made up of single row, but shorter than paroral, spoon-shaped because anterior portion concave right of small, ellipsoidal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depression slightly reminiscent of the large cavity found in *Steinia* (Foissner 1989; for review, see Berger 1999, p. 624). Pharyngeal fibres long, originate at proximal end of paroral and endoral and from adoral zone (Fig. 57c, o, r, s).

Cirral pattern rather constant (Fig. 57o, s, u, 57a, c–e). All cirri only about 7 µm long and of similar structure, that is, composed of two rows of basal bodies comprising three (mostly two in posterior third of cell) cilia. Three frontal cirri along oblique, distal portion of adoral zone. Distance between cirri I/1 and II/3 smaller than that between II/3 and III/3; middle cirrus (II/3) somewhat larger (nine cilia) than other cirri. Buccal cirrus composed of 2–3 cilia only and thus very indistinct, right of anterior portion of paroral. Usually one, sometimes up to five parabuccal cirri behind right frontal cirrus. Frontoventral row composed of 25 cirri on average, commences close to distal end of adoral zone, extends more or less in parallel to right marginal row far more posteriorly than buccal vertex, that is, ends at 23% of body length on average in protargol preparations. Frontoterminal cirri, postoral ventral cirri, pretransverse ventral cirri, and transverse cirri lacking. Right marginal row commences dorsally, extends more or less along right cell margin to near rear cell end; posteriorly distinctly separated from left marginal row, which ends about at same level.

Dorsal bristles about 4 µm long, arranged in three kineties (Fig. 57p, t, v). Kinety 1 terminating in anterior third of cell or near mid-body, composed of 19 and 10 bristles, respectively, in specimens shown in Fig. 57p, t; sometimes a second short row present. Kineties 2 and 3 almost bipolar. Kineties mainly made of paired basal bodies, the anterior, rarely also the posterior ciliated. Usually, some bristle complexes composed of four basal bodies interspersed between paired ones.

Cell division (Fig. 59a–q): Foissner (1994a) described and illustrated this part of the life cycle in great detail. In the present review, only the most important details are described. Generally, the process proceeds relatively simple because the infraciliature is distinctly reduced in *Circinella*.

Body shape. Dividers become rather short and broad (Table 21). When the oral primordium is formed the rear third of the cell becomes globular (Fig. 59a). Subsequently, the middle portion broadens, making early and middle dividers spindle-shaped (Fig. 59c, e, h). Late dividers are more or less ellipsoidal, and postdividers are roughly pisciform (Fig. 59k, m, p). The changes are, at least partially, due to a slow spiral contraction by about 180°. Thus, the oral areas of the filial products face opposite directions (e.g., Fig. 59k–n).

Oral apparatus and frontoventral cirri. The oral primordium originates in mid-body, that is, without contact to parental cirri (Fig. 59a, b). Later it becomes very

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← **Fig. 57o–r** *Circinella arenicola* (from Foissner 1994a. Protargol impregnation). **o–q:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 450 µm. Arrow in (o) marks gap in adoral zone. For detailed labelling of cirral pattern see (s, t). **r:** Oblique ventral view of proximal portion of oral apparatus, 45 µm. AM = adoral membranelles, D = shallow depression, E = endoral, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = right marginal row, 1–3 = dorsal kineties. Page 317.

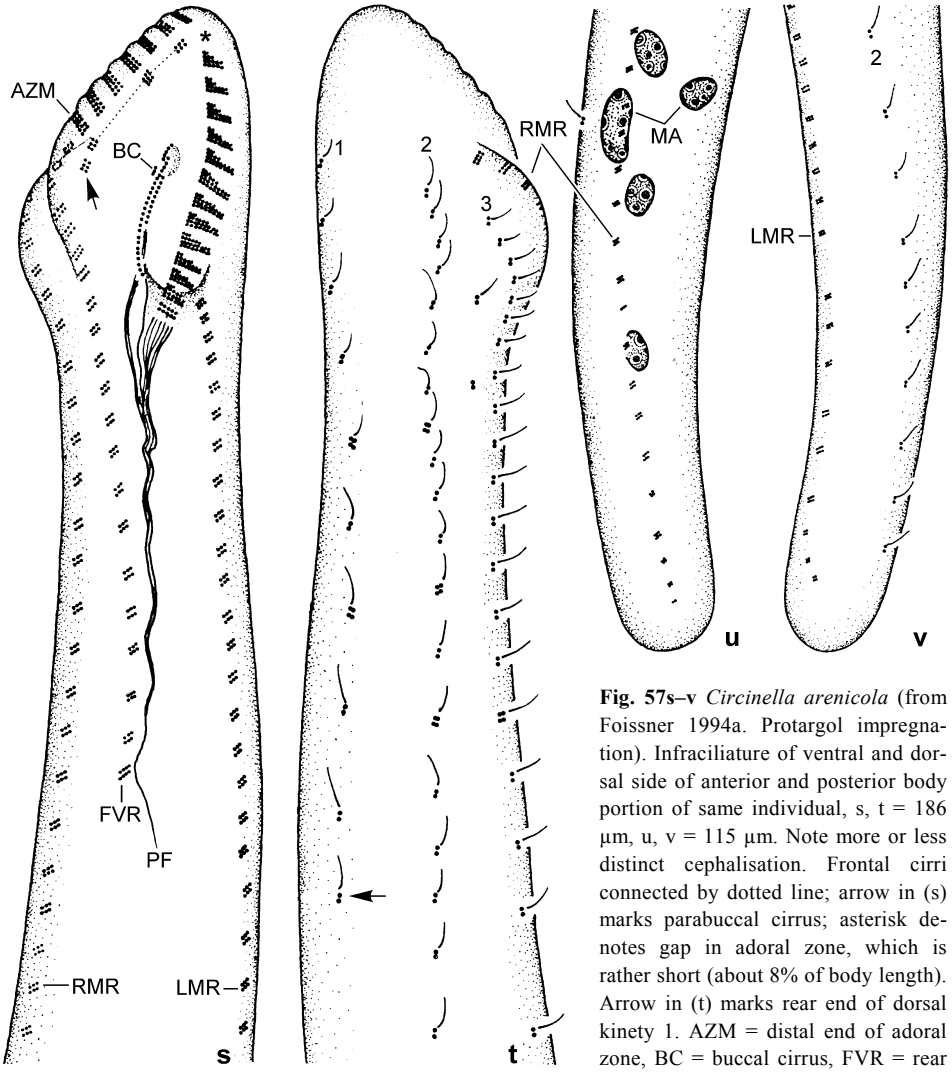

Fig. 57s–v *Circinella arenicola* (from Foissner 1994a. Protargol impregnation). Infraciliature of ventral and dorsal side of anterior and posterior body portion of same individual, s, t = 186 µm, u, v = 115 µm. Note more or less distinct cephalisation. Frontal cirri connected by dotted line; arrow in (s) marks parabuccal cirrus; asterisk denotes gap in adoral zone, which is rather short (about 8% of body length). Arrow in (t) marks rear end of dorsal kinety 1. AZM = distal end of adoral zone, BC = buccal cirrus, FVR = rear end of frontoventral row, LMR = left marginal row, MA = macronuclear nodules, PF = pharyngeal fibres, RMR = right marginal row, 1–3 = dorsal kineties. Page 317.

long because it extends anteriorly to near the parental oral apparatus (Fig. 59c, d). Next, this long anlage splits; the anterior portion fuses with the frontoventral anlagen of the proter; the left part of the posterior primordium produces the adoral zone of the opisthe, and the right portion forms four cirral streaks for the opisthe (Fig. 59e–j). No parental cirri are involved in primordia formation in the opisthe. The anlagen I–IV of the opisthe form, as expected, (i) the undulating membranes and the left frontal cirrus; (ii) the middle frontal cirrus and the buccal cirrus; (iii) the right

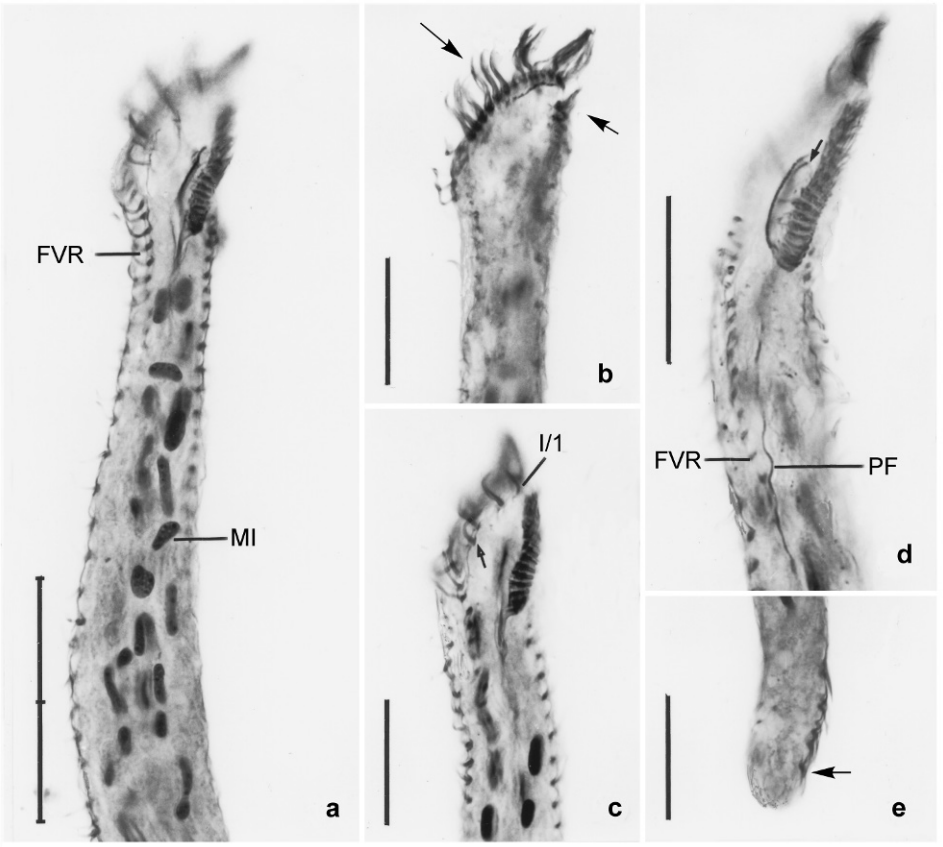

Fig. 58a–e *Circinella arenicola* (from Foissner 1994a. Protargol impregnation). **a, b:** Ventral view of broadened "head-region". Short arrow in (b) marks proximal portion, long arrow denotes distal portion of adoral zone. **c:** Infraciliature of ventral side of indistinctly cephalised individual. Arrow marks parabuccal cirrus. **d:** Oblique ventral view showing (relatively indistinctly) endoral and shallow depression nearby (arrow). **e:** Rear cell end showing that the marginal rows end subterminally (arrow). FVR = frontoventral row, I/1 = left frontal cirrus, MI = micronucleus, PF = pharyngeal fibres. Scale bar division = 20 µm. Page 317.

frontal cirrus and 1–5 parabuccal cirri; and (iv) the frontoventral row. For a brief discussion which of the ordinary six anlagen (I–VI) are lacking in *Circinella*, see remarks at genus section. The parental frontal cirri produce short streaks (Fig. 59e, f), but remain intact and are still recognisable in middle dividers (Fig. 59k). The parental frontoventral row is not involved in primordia formation and is resorbed while the new row is formed from the anlagen of the frontal cirri and oral primordium of the opisthe (Fig. 59d, f, i, k). Usually, supernumerary frontal and parabuccal cirri occur in anlagen I–III of both filial products, often persisting in late dividers and even in young postdividers (Fig. 59p). The undulating membranes, which are formed as is usual from anlage I, develop side by side and get at their final positions only af-

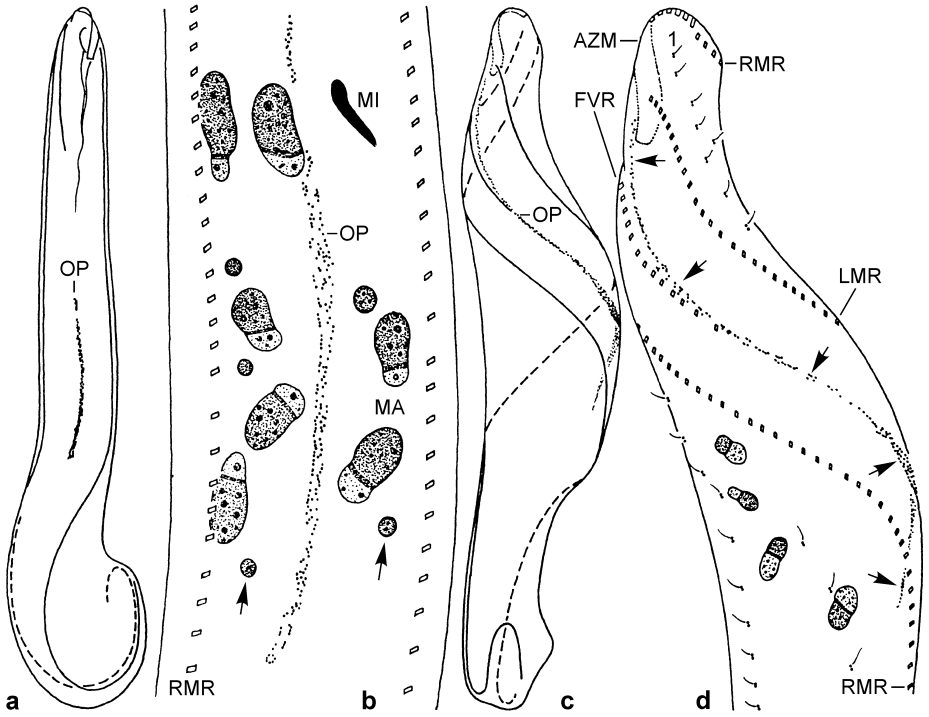

Fig. 59a–d *Circinella arenicola* (from Foissner 1994a. Very early morphogenetic stages after protargol impregnation). **a, b:** Morphogenesis begins with the apokinetal formation of a long oral primordium in mid-body (a = 247 µm). Some macronuclear nodules degenerate (arrows in b). **c, d:** The oral primordium elongates and extends from mid-body, which becomes broader, to near the parental oral apparatus (arrows in d; c = 224 µm). AZM = adoral zone of membranelles, FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodules, MI = micronucleus, OP = oral primordium, RMR = right marginal row. Page 317.

ter completion of cytokinesis. The endoral migrates into the buccal cavity, seemingly optically crossing the paroral (Fig. 59p). The gap in the adoral zone disappears in early dividers, that is, when the cells start to contract (Fig. 59d, f). It appears only after division when the cells become long and the anterior end broadens.

Marginal cirri and dorsal kineties. The marginal rows are formed as is usual by intrakinetal anlagen at two levels within each row (Fig. 59k–n). The formation of the dorsal infraciliature could not be studied in every detail. However, according to Foissner (1994a) (i) dorsomarginal kineties are not formed; (ii) caudal cirri are lacking; (iii) kinety 1 probably is formed de novo, similar (but likely not homologous; see remarks at genus section) as in *Engelmanniella*, that is, without participation of parental kinety 1; (iv) the other kineties obviously originate by intrakinetal proliferation of dikinetids; (v) both basal bodies become ciliated in developing and even in parental kinetids during cell division (Fig. 59k–q).

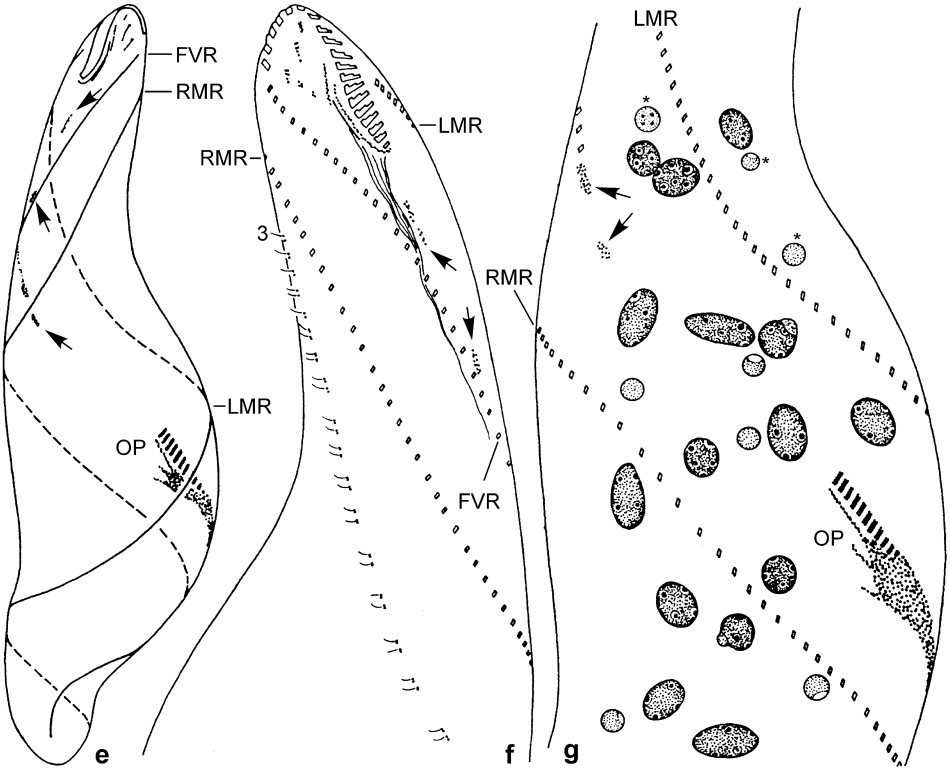

Fig. 59e–g *Circinella arenicola* (from Foissner 1994a. Protargol impregnation. Parental structures shown by contour). Early morphogenetic stage (e, overview; 192 µm) after division of oral primordium into anterior portion (arrows) and a more prominent posterior portion (OP). Note that many macronuclear nodules degenerate (small globules). FVR = frontoventral row, LMR = left marginal row, OP = oral primordium, RMR = right marginal row, 3 = dorsal kinety 3. Page 317.

Nuclear apparatus. As is usual, the macronuclear nodules have a replication band and most macronuclear nodules fuse to a single, globular mass in middle dividers (Fig. 59b, d). Somewhat later, the fused macronucleus elongates and fragments during cytokinesis (Fig. 59k, o, q). The micronuclei divide in the usual way (Fig. 59k, o, q). Some of the many macronuclear nodules degenerate in almost all dividers. These nodules are spherical, small, and usually faintly impregnated; often they have a clear, unstained cap and/or a few sharply stained granules inside (Fig. 59g, o).

Resting cyst: *Circinella arenicola* forms resting cysts because the sample was completely dry before it was rewetted (Foissner 1994a).

Occurrence and ecology: *Circinella arenicola* is obviously very rare, because as yet found only at the type locality, namely the Coral Park Sand Dunes, about 25 km west of Rockville, Zion National Park, Utah, USA (Foissner 1994a, Foissner et al. 2008, p. 353). *Circinella arenicola* is, due to its size (200–600 µm long) and filiform

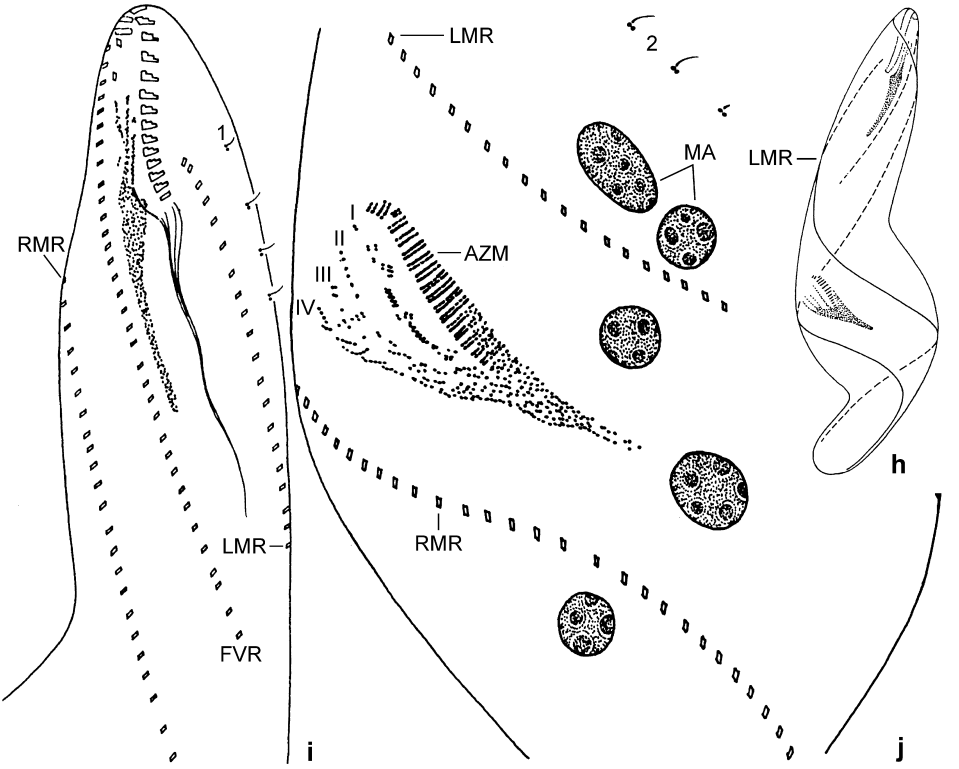

Fig. 59h–j *Circinella arenicola* (from Foissner 1994a. Protargol impregnation. Parental structures shown by contour). Middle divider in overview (h = 180 µm) and details showing anlagen for proter (i) and opisthe (j). Note that the parental frontoventral row is not involved in primordia formation. Further details, see text. AZM = adoral zone of opisthe, FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodules, RMR = right marginal row, I–IV = frontal-ventral cirri anlagen of opisthe, 1 = dorsal kinety 1, 2 = dorsal kinety 2(?). Page 317.

shape, an eye-catching species which is very likely confined to terrestrial habitats of the Holarctis (Foissner 1994a, c, 1998), perhaps even to sand dunes in North America (Foissner et al. 2008, p. 353), because it was not recorded during a detailed survey of the Namib Desert (Foissner et al. 2002a) or other similar biotopes in other continents (e.g., Blatterer & Foissner 1988).

The sand sample, which was collected in June 1989, contained much plant debris which was enriched by sieving (Foissner 1994a); dune vegetation was sparse and restricted mainly to *Nerisyrenia camporum* (bicolor fanmustard). *Circinella arenicola* excysted 14 d after rewetting the sample (pH 5.6) and became very abundant 4 d later when the water of the moistened sample turned yellowish and slightly viscous by leached substance from plant debris. This behaviour indicates that *C. arenicola* is active mainly after longer periods of rain (Foissner 1994a). Feeds on bacteria (Foissner 1994a). Biomass of 10^6 specimens about 120 mg (Foissner 1998, p. 200).

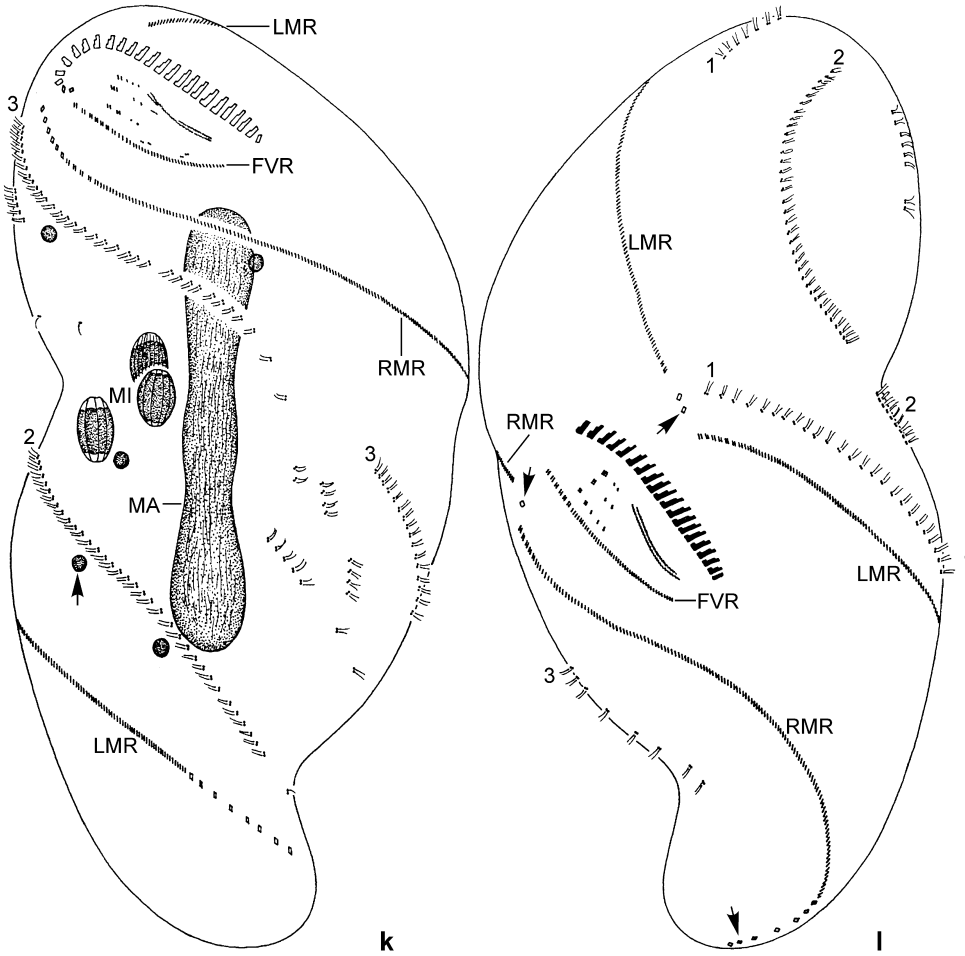

Fig. 59k, l *Circinella arenicola* (from Foissner 1994a. Protargol impregnation. Parental structures white, new black). Middle divider (130 µm) with fused macronucleus showing oral area of proter (k) and opisthe (l). Some macronuclear nodules degenerate (arrow in k). Arrows in (l) denote some parental left and right marginal cirri. FVR = new frontoventral rows, LMR = new left marginal rows, MA = fused macronucleus, MI = micronuclei, RMR = new right marginal rows, 1–3 = new dorsal kineties. Page 317.

Circinella vettersi (Berger & Foissner, 1989) Foissner, 1994
(Fig. 60a–h, Table 21)

1989 ***Hemisincirra vettersi* nov. spec.**[1] – Berger & Foissner, Bull. Br. Mus. nat. Hist. (Zool.), 55: 35, Fig. 49–55, Table 9 (Fig. 60a–h; original description; the holotype slide [accession number 1988:2:1:11]

[1] Berger & Foissner (1989a) provided the following diagnosis: Theront in vivo about 150 × 9 µm, extremely vermiform. Trophont in vivo about 125–160 × 14–25 µm. About 6 contractile vacuoles near left body margin. 27 macronuclear segments and 8 adoral membranelles on average. 3 dorsal kineties of body length.

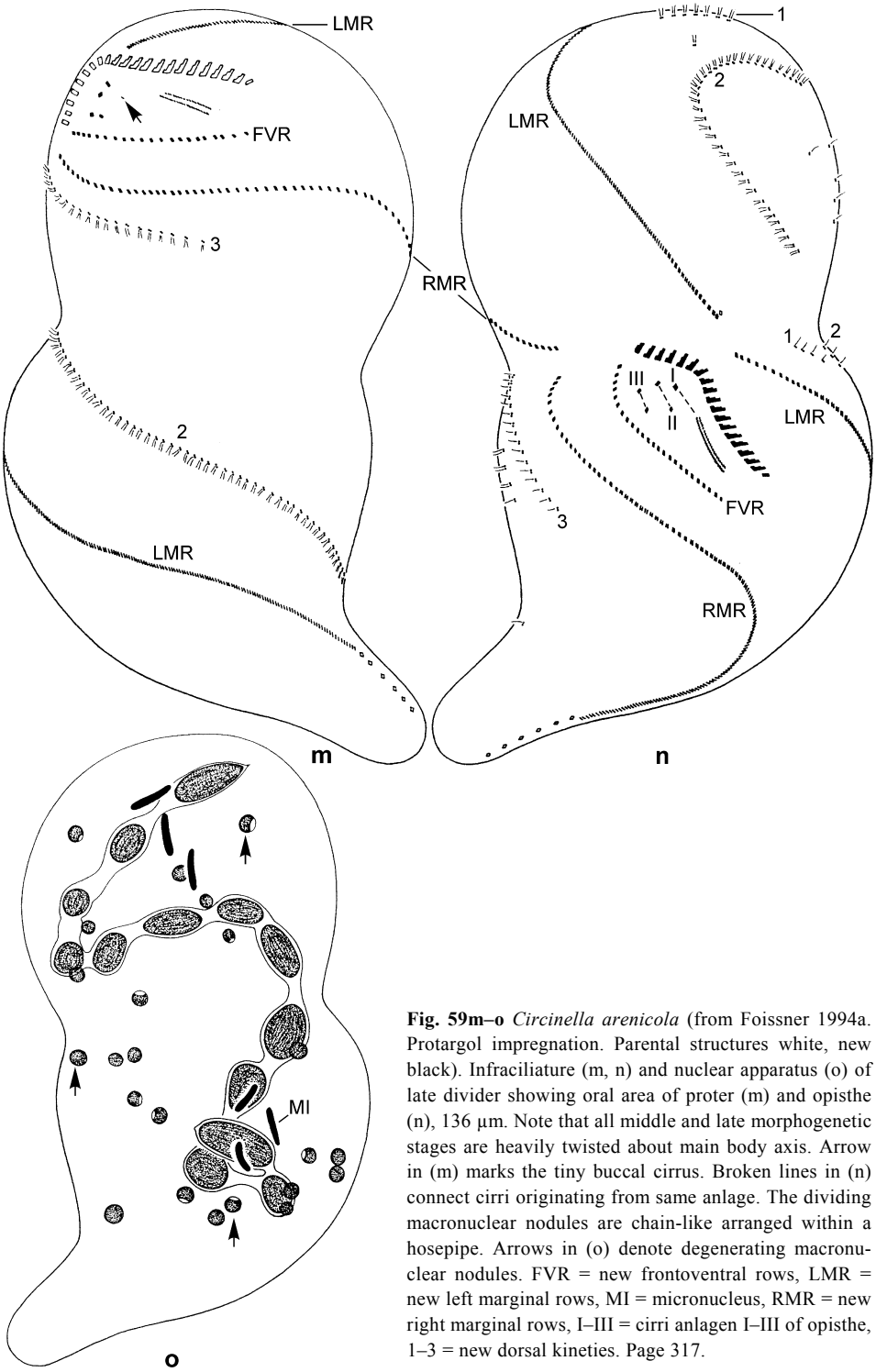

Fig. 59m–o *Circinella arenicola* (from Foissner 1994a. Protargol impregnation. Parental structures white, new black). Infraciliature (m, n) and nuclear apparatus (o) of late divider showing oral area of proter (m) and opisthe (n), 136 µm. Note that all middle and late morphogenetic stages are heavily twisted about main body axis. Arrow in (m) marks the tiny buccal cirrus. Broken lines in (n) connect cirri originating from same anlage. The dividing macronuclear nodules are chain-like arranged within a hosepipe. Arrows in (o) denote degenerating macronuclear nodules. FVR = new frontoventral rows, LMR = new left marginal rows, MI = micronucleus, RMR = new right marginal rows, I–III = cirri anlagen I–III of opisthe, 1–3 = new dorsal kineties. Page 317.

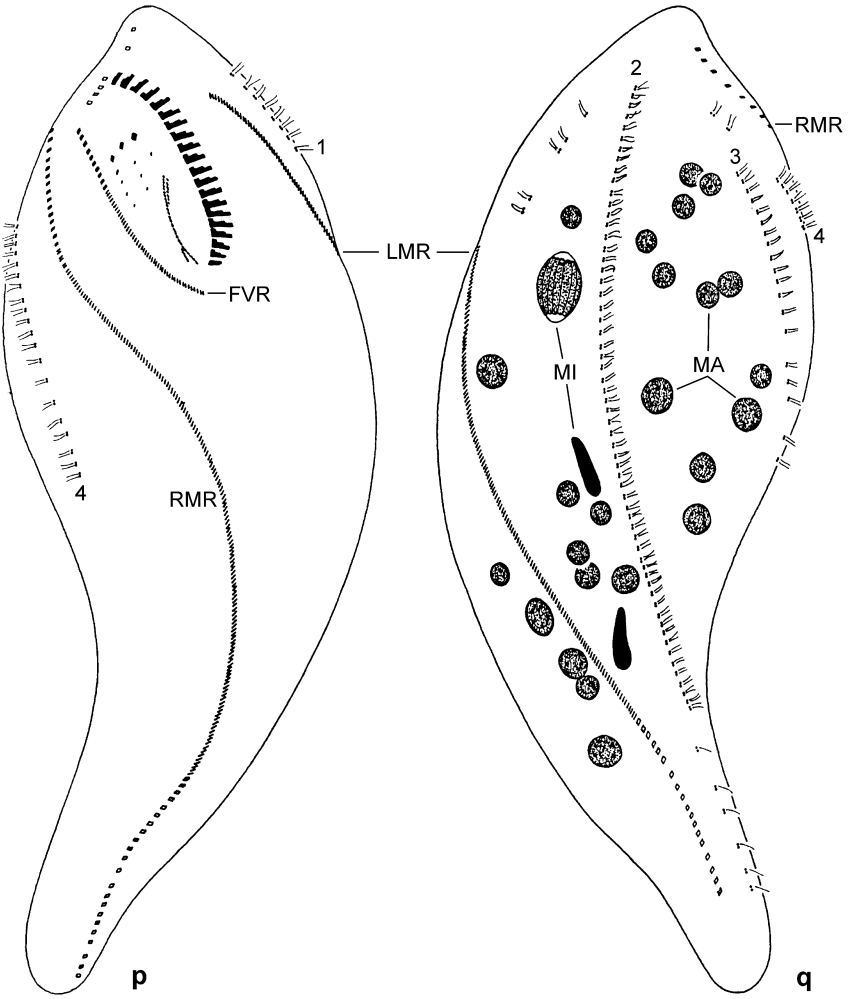

Fig. 59p, q *Circinella arenicola* (from Foissner 1994a. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of postdivider (opisthe), 130 µm. FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodules, MI = micronuclei, RMR = right marginal row, 1–4 = dorsal kineties. Page 317.

and a paratype slide [1988:2:1:12] have been deposited in the British Museum of Natural History, London; Berger & Foissner 1989a, p. 20).

1994 ***Circinella vettersi* (Berger & Foissner, 1989) nov. comb.** – Foissner, Europ. J. Protistol., 30: 169 (combination with *Circinella*).

2001 ***Circinella vettersi* (Berger and Foissner, 1989) Foissner, 1994** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 31 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: Berger & Foissner (1989a) dedicated this species to Wolfgang Vetters (University of Salzburg), who collected the soil sample containing this species from Iceland.

Remarks: There are several vermiform species, besides the congeners (see key for separation), which resemble *C. vettersi* at superficial observation. Note that only some differences are mentioned; for details of compared species, see reviews or original descriptions. *Hemisincirra vermicularis* Hemberger, 1985 (for review, see Berger 2008, p. 435) has only one dorsal kinety (vs. 3), about 10 serially arranged macronuclear nodules (vs. about 27), about 12 adoral membranelles (vs. about eight), and two cirri behind the right frontal cirrus (vs. 0). Perhaps there exist some further differences (buccal cirrus perhaps absent vs. present; 4 contractile vacuoles vs. 6). *Hemisincirra interrupta* (Foissner, 1982) Foissner in Berger 2001 has only one dorsal kinety and one contractile vacuole, about 14 adoral membranelles, and frontoterminal cirri are present (vs. lacking; for review, see Berger 2008, p. 432). *Hemisincirra inquieta* Hemberger, 1985 is, inter alia, somewhat smaller (around 110 µm long) and has cortical granules along the cirri and dorsal bristles (for review, see Berger 2008, p. 403). *Hemisincirra rariseta* Foissner et al., 2002a has, inter alia, more adoral membranelles (16 vs. 8), less macronuclear nodules (16 vs. about 27), and only two dorsal kineties (for review, see Berger 2008, p. 428). *Hemiurosoma polynucleatum* (Foissner, 1984) Foissner et al., 2002a has, inter alia, 6–9 macronuclear nodules, four dorsal kineties including a dorsomarginal kinety, a postoral ventral cirrus, and a continuous adoral zone composed of much more (21) membranelles (for review, see Berger 1999, p. 419; 2008, p. 634). *Vermioxytricha* species have a short dorsomarginal kinety, the frontoventral cirri not in a single row, and frontoterminal cirri – a group of cirri lacking in *Circinella* (for review of *Vermioxytricha*, see Berger 2008, p. 596). *Engelmanniella mobilis* has, inter alia, more cirral rows, some of which are from the parental and grandparental generation and thus composed of widely spaced cirri (see p. 502).

Morphology: Slender specimens in life about 150 × 9 µm, length:width ratio about 16.6:1 in life, about 12:1 on average in protargol preparations (Table 21), that is, body more or less very slender vermiform, usually S-shaped and posteriorly tapered (Fig. 60a, b). Well-nourished specimens in life about 125–160 × 14–25 µm, distinctly twisted, nematode-like (Fig. 60c, d). Frontal area very thin, remaining body not flattened dorsoventrally. Body very fragile, that is, extremely difficult to observe in life because it is disintegrated after applying the cover-glass. Macronuclear nodules and micronuclei roughly arranged in central body portion, that is, in area where contractile vacuoles occur (Fig. 60a, f); individual nodules and micronuclei elongated and roughly of similar size. About six contractile vacuoles near left body margin (Fig. 60b). Cortical granules lacking. Cytoplasm colourless, in well-nourished individuals with many fat globules about 10 µm across. Slender specimens with worm-like movements, well-nourished cells nearly motionless.

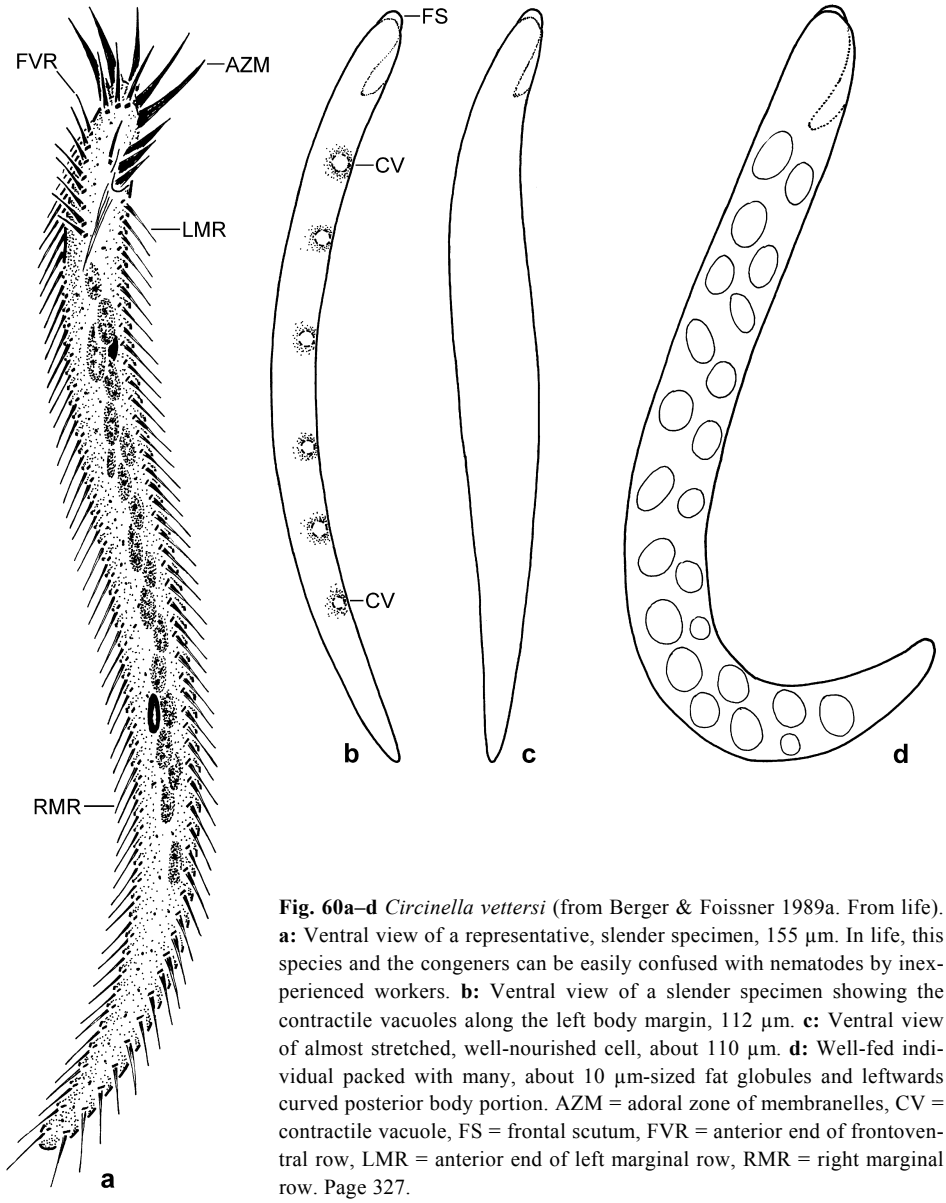

Fig. 60a–d *Circinella vettersi* (from Berger & Foissner 1989a. From life). **a:** Ventral view of a representative, slender specimen, 155 µm. In life, this species and the congeners can be easily confused with nematodes by inexperienced workers. **b:** Ventral view of a slender specimen showing the contractile vacuoles along the left body margin, 112 µm. **c:** Ventral view of almost stretched, well-nourished cell, about 110 µm. **d:** Well-fed individual packed with many, about 10 µm-sized fat globules and leftwards curved posterior body portion. AZM = adoral zone of membranelles, CV = contractile vacuole, FS = frontal scutum, FVR = anterior end of frontoventral row, LMR = anterior end of left marginal row, RMR = right marginal row. Page 327.

Adoral zone occupies only 6% of body length on average, that is, extremely short, composed of only eight membranelles (Fig. 60a, e, g). Distal membranelles loosely arranged; probably all membranelles composed of two rows of basal bodies only. Buccal area very small and undulating membranes very inconspicuous, thus structures could not be clearly seen in the light microscope. Cytopharynx extends obliquely backwards.

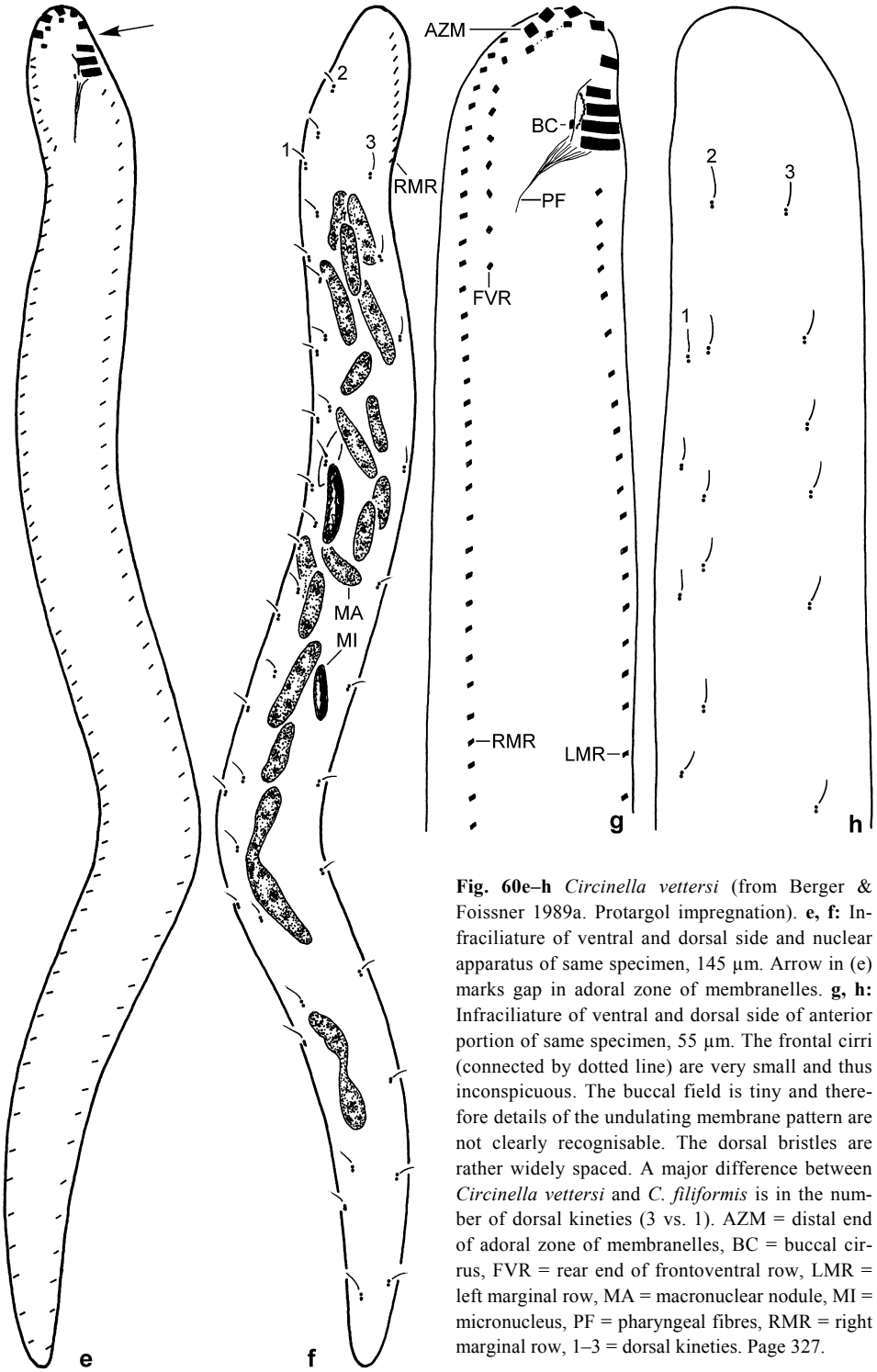

Fig. 60e–h *Circinella vettersi* (from Berger & Foissner 1989a. Protargol impregnation). **e, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 145 µm. Arrow in (e) marks gap in adoral zone of membranelles. **g, h:** Infraciliature of ventral and dorsal side of anterior portion of same specimen, 55 µm. The frontal cirri (connected by dotted line) are very small and thus inconspicuous. The buccal field is tiny and therefore details of the undulating membrane pattern are not clearly recognisable. The dorsal bristles are rather widely spaced. A major difference between *Circinella vettersi* and *C. filiformis* is in the number of dorsal kineties (3 vs. 1). AZM = distal end of adoral zone of membranelles, BC = buccal cirrus, FVR = rear end of frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, PF = pharyngeal fibres, RMR = right marginal row, 1–3 = dorsal kineties. Page 327.

Three inconspicuous frontal cirri behind distalmost adoral membranelles (Fig. 60e, g). Buccal cirrus close to buccal vertex, that is, near rear end of undulating membranes. Frontoventral row composed of eight cirri and terminating at 11% of body length on average (Table 21); cirri very regularly arranged, form continuous row. Parabuccal cirri, frontoterminal cirri, postoral ventral cirri, pretransverse ventral, and transverse cirri lacking. Right marginal row commences near distal end of adoral zone, ends – like left row – at/near rear cell end. Left row begins near buccal vertex. Distinctly more right than left marginal cirri. All cirri very thin.

Dorsal bristles arranged in three more or less bipolar kineties (Fig. 60f, h). Bristles about 2–3 µm long in protargol preparations. Distance between kinety 1 and 2 distinctly smaller than that between kineties 2 and 3. Caudal cirri very likely lacking.

Occurrence and ecology: *Circinella vettersi* is very likely confined to terrestrial habitats, that is, has a high degree of soil autochthonism; reliable recorded from the Holarctis, Palaeotropis, and Neotropis (Foissner 1998). Type locality is an postglacial basal desert (340 m sea-level) near Dettifos (Neisland, Iceland), where it occurred in a soil sample (pH 6.2) with tufts of *Alchemilla alpina* (Berger & Foissner 1989a). Biomass of 10^6 specimens about 23 mg (Foissner 1998, p. 200).

Circinella filiformis (Foissner, 1982) Foissner, 1994
(Fig. 61a–l, Table 21)

1982 ***Perisincirra filiformis* nov. spec.**[1] – Foissner, Arch. Protistenk., 126; 99, Abb. 27a–i, 69, 70, Tabelle 23 (Fig. 61a–j; original description; the holotype slide [accession number 1981/98] has been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Aescht 2008, p. 155).

1984 ***Hemisincirra filiformis* (Foissner, 1982) nov. comb.** – Foissner, Stapfia, 12: 119 (invalid combination with *Hemisincirra*, see nomenclature).

1994 ***Circinella filiformis* (Foissner, 1989) nov. comb.** – Foissner, Europ. J. Protistol., 30: 169 (combination with *Circinella*).

2001 ***Circinella filiformis* (Foissner, 1982) Foissner, 1994** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 71 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2009 ***Circinella filiformis*** – Foissner, Protozoological Monographs, 4: 212, Fig. 5 (Fig. 61a; review on soil ciliates).

Nomenclature: No derivation of the species-group name is given in the original description. The name *filiform·is*, *-is*, *-e* (Latin adjective [m; f; n]; filiform, filamen-

[1] Foissner (1982) provided the following diagnosis: *In vivo* etwa 150–250 × 10–20 µm große *Perisincirra* mit einer *in vivo* etwa 30 µm langen Frontalreihe und kettenförmigem, aus durchschnittlich 16 ellipsoiden Nodien aufgebautem Makronucleus. Adorale Membranellenzone kürzer als die Frontalreihe, nimmt ungefähr ein Dreizehntel der Gesamtlänge des Tieres ein. Durchschnittlich 10 adorale Membranellen, von denen die vorderen 3 durch eine breite Lücke von den hinteren getrennt sind. 1 Dorsalkinete nahe des rechten Körperrandes. Theront fadenförmig, nach hinten keilförmig verschmälert, häufig leicht S-förmig gebogen. Trophont im hinteren Drittel stets mehr oder minder deutlich nach links gebogen, lang spindelförmig, sehr träge und daher ausgeprägt nematodenartig.

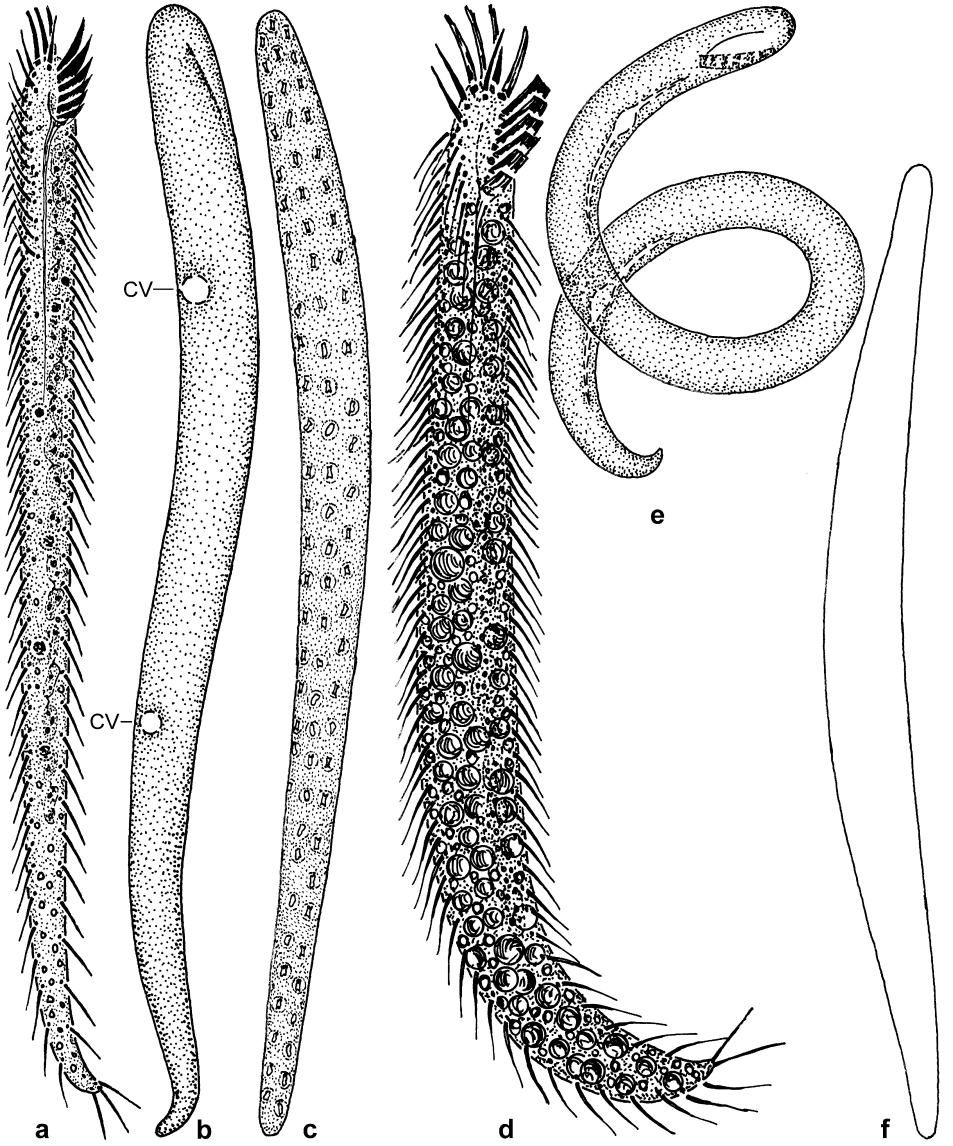

Fig. 61a–f *Circinella filiformis* (from Foissner 1982. From life). **a:** Ventral view of a representative, slender specimen, 210 µm. **b:** Dorsal view of a slender cell showing the two contractile vacuoles, 195 µm. **c:** Lateral view of a slender specimen showing the yellowish crystals enclosed in vacuoles arranged in longitudinal rows. **d:** Ventral view of a well-fed cell, about 180 µm. **e:** Spiralled, well-nourished specimen looking like a nematode at superficial observation. **f:** Lateral view of well-nourished specimen, about 180 µm. CV = contractile vacuole. Page 333.

tous; Hentschel & Wagner 1996, p. 252) obviously alludes to the very slender body shape. Foissner (1984) transferred this and some other "*Perisincirra*" species de-

scribed by Foissner (1982) to *Hemisincirra* before this genus was established by Hemberger (1985). Berger (2001, p. 71, 72) corrected this mistake for most species, but not for the present one because it is obviously properly classified in *Circinella* since 1994. However, when one prefers a classification in *Hemisincirra*, it has to be combined with this genus formally.

Remarks: *Hemisincirra interrupta* (Foissner, 1982) Foissner in Berger, 2001 is very similar to the present species as concerns body shape, nuclear apparatus, and dorsal infraciliature (for review, see Berger 2008, p. 432). On average it has about two times more macronuclear nodules (30 vs. 16) and the frontoventral row is shorter than the adoral zone (vs. longer). In addition, *Hemisincirra interrupta* has two cirri right of the anterior portion of the frontoventral row. Unfortunately, it is not known whether these are frontoterminal cirri or the anterior, setoff portion of the right marginal row. Ontogenetic and relevant molecular data are needed to check the generic classification (*Hemisincirra* or *Circinella*) of this species. *Hemisincirra rariseta* has two dorsal kineties (vs. 1) and the frontoventral row is somewhat irregular against continuous in *C. filiformis*, indicating that it originates from more than one anlage. *Hemisincirra vermicularis* has four contractile vacuoles (vs. two) and the frontoventral row is – as in *H. rariseta* – shorter than the adoral zone.

Morphology: Body size in life 150–250 × 10–20 µm, length:width ratio 15:1 on average in protargol preparations (Table 21). Body filiform, anterior end narrowly rounded, posterior portion tapered and almost always curved leftwards; body only in frontal area slightly flattened dorsoventrally. Two forms (slender specimens, termed theront in original description; well-nourished cells, termed trophont in original description) occur, differing mainly in body shape (Fig. 61a–f). Slender specimens transparent, filiform and cuneiform narrowed posteriorly, often slightly S-shaped; frontal area with distinct furrow on right dorsomarginal side (Fig. 61e). Well-nourished specimens opaque, long fusiform, rear third more or less distinctly curved leftwards, very sluggish and therefore pronounced nematode-like (Fig. 61d). All transitions between slender and well-nourished individuals occur so that it can be excluded that these are two species; remaining features and infraciliature very similar. Nuclear apparatus composed of 16 macronuclear nodules and two micronuclei on average, chain-like arranged in central body portion slightly left of midline. Individual macronuclear nodules 6.6 × 3.3 µm, often connect by fine thread. Each one micronucleus in anterior and posterior body portion. Two contractile vacuoles, about at 25% and 65% of body length; collecting canals short and difficult to recognise. Cortical granules lacking. Pellicle colourless, close underneath rows of small vacuoles containing yellowish crystals (Fig. 61c). Endoplasm of slender specimens with some highly refractive granules in posterior portion. Well-fed cells packed with shining, colourless globules 1–6 µm across (Fig. 61d). Food vacuoles about 3 µm across, with unknown content. Movement slow, often snake-like.

Adoral zone occupies only about 7% of body length, composed of 10 membranelles on average; distal three membranelles separated from proximal membranelles by distinct gap. Bases of largest membranelles only about 2 µm wide in life. One

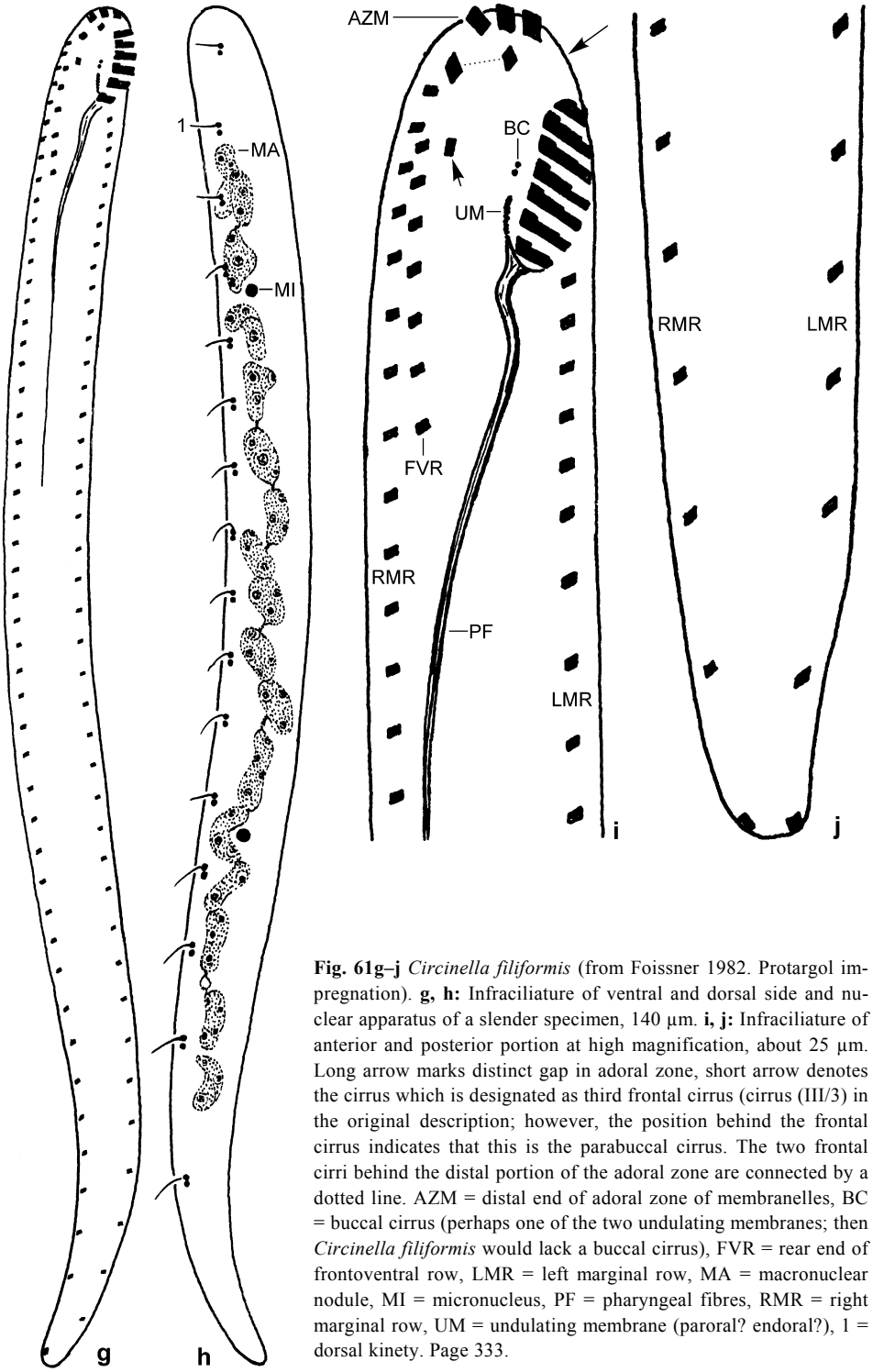

Fig. 61g–j *Circinella filiformis* (from Foissner 1982. Protargol impregnation). **g, h:** Infraciliature of ventral and dorsal side and nuclear apparatus of a slender specimen, 140 µm. **i, j:** Infraciliature of anterior and posterior portion at high magnification, about 25 µm. Long arrow marks distinct gap in adoral zone, short arrow denotes the cirrus which is designated as third frontal cirrus (cirrus (III/3) in the original description; however, the position behind the frontal cirrus indicates that this is the parabuccal cirrus. The two frontal cirri behind the distal portion of the adoral zone are connected by a dotted line. AZM = distal end of adoral zone of membranelles, BC = buccal cirrus (perhaps one of the two undulating membranes; then *Circinella filiformis* would lack a buccal cirrus), FVR = rear end of frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, PF = pharyngeal fibres, RMR = right marginal row, UM = undulating membrane (paroral? endoral?), 1 = dorsal kinety. Page 333.

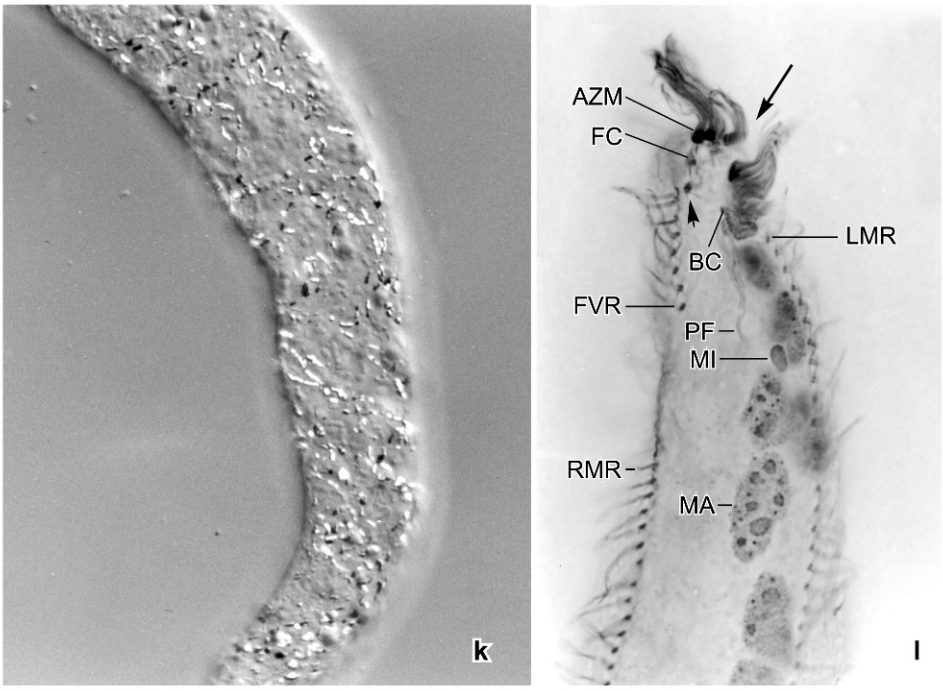

Fig. 61k, l *Circinella filiformis* (original micrographs, kindly supplied by W. Foissner, from the Müllerboden population recorded by Foissner et al. 2005. k, interference contrast; l, protargol impregnation). **k:** Rear body portion showing the slender body and the structure of the cytoplasm. **l:** Infraciliature of anterior body portion in ventral view. Long arrow marks distinct gap in adoral zone, short arrow marks the cirrus whose designation (right frontal cirrus? parabuccal cirrus?) is not certain. AZM = adoral zone of membranelles, BC = buccal cirrus (or one of the two undulating membranes?), FC = frontal cirrus, FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, PF = pharyngeal fibres, RMR = right marginal row, UM = undulating membrane (paroral? endoral?). Page 333.

short, indistinct undulating membrane right of proximal portion of adoral zone, according to original description this is the paroral (however, it cannot be excluded that this is the endoral). In addition, Foissner (1982) discussed that the two basal bodies ahead of this membrane could be the endoral.[1] Buccal field very small and flat and thus inconspicuous. Pharyngeal fibres conspicuously strong, extend almost to near cell centre (Fig. 61g).

Cirral pattern basically as in type species, but frontal ciliature somewhat deviating from congeners because only two frontal cirri immediately behind distal portion of adoral zone; which of the ordinary three frontal cirri (I/1; II/3; III/3) is lacking is not known. According to Foissner (1982), the cirrus left of the anterior end of the frontoventral row is the third (III/3; right) frontal cirrus. I suppose that it is the para-

[1] For that case, Foissner (1982) assumed that the cirrus (Fig. 61i, short arrow) left of the anterior portion of the frontoventral row could be the buccal cirrus.

buccal cirrus (III/2), that is, *Circinella filiformis* very likely lacks one frontal cirrus. Buccal cirrus very small, that is, composed of only two basal bodies, ahead of short undulating membrane; whether the two basal bodies are in fact the buccal cirrus or one of the two undulating membranes is not known, that is, more detailed studies, including ontogenetic ones, are needed for correct interpretation of cirral pattern. Frontoventral row composed of about eight cirri, commences about at level of cirrus III/2 (see above for uncertainty about designation), terminates at 15% of body length on average (Table 21). Frontoterminal, postoral ventral, pretransverse ventral, and distinct transverse cirri lacking. Right marginal row commences near frontal cirri, terminates, like left row, at rear cell end; left row begins at level of buccal vertex. Marginal cirri about 10 µm long, distance between cirri posteriorly about thrice as large as anteriorly. Whether the cirri at the rear cell end are marginal and/or transverse and/or caudal cirri is not known; for correct interpretation and designation, ontogenetic data are needed.

Dorsal bristles about 3 µm long, arranged in only one bipolar kinety close to left[1] cell margin; bristles about equally spaced (Fig. 61h). Presence/absence of caudal cirri not known (see previous paragraph).

Conjugation: Conjugating specimens fuse, as is usual, at adoral zone (Foissner 1982).

Occurrence and ecology: *Circinella filiformis* is very likely confined to terrestrial habitats (Foissner 1998, p. 200). Characteristic for mull and mor soils (Foissner 1987a, p. 153; 1999a, p. 104; Aescht & Foissner 1993). Type locality is a mesoxerophytic grassland (48°21'N 15°54'E; co-ordinates from Aescht 2008, p. 155) near the village of Zwentendorf, Lower Austria (Foissner 1982); it was moderately abundant. More details on the type locality ("Profil 1, Heißlände Althann") and on other sites in the same area where *C. filiformis* was found, see Foissner et al. (1985, p. 108). Further reliable records from terrestrial habitats: with low relative abundance (0.1%) in an acid alpine pasture from the Schloßalm area near the village of Bad Hofgastein, Salzburg, Austria (Berger et al. 1986, p. 268); subalpine grassland field trial near the village of Aigen, Styria, Austria (Foissner et al. 1990, p. 18); soil from Norway spruce stands (*Picea abies*) in the Upper Austrian Part of the Bohemian Forest (Aescht & Foissner 1993, p. 328); several forest soils (*Luzulo-Fagenion*; *Pruno-Fraxinetum*; *Euphorbio saxatilis-Pinetum nigrae*) in Eastern Austria (Foissner et al. 2005, p. 625); beech forest soil (pH 4.4) and very acid soil (pH 3.1) from a pine forest near the city of Ulm, Germany (Lehle 1989, p. 141; Funke 1986, p. 71); with a dominance of 2.5% in a young, white-dune soil with very low content of organic matter in Norderney (about 53°43'N 07°12'E), an East Friesian Island, Germany (Goralczyk & Verhoeven 1999, p. 110; Verhoeven 2001, p. 27; 2001a, p. 392; 2002, p. 189; Foissner & AL-Rasheid 2007, p. 203); soil stressed by textile industry in Nordhorn, Germany (Niebuhr 1989, p. 81; identification checked by W. Foissner; obviously incorrectly spelled *Hemisincirra fililormis*; for review of German records,

[1] According to the original description (Foissner 1982), the dorsal kinety is close to the right body margin (Fig. 61h).

see Foissner 2000a, p. 256); soil from fields in the village of Ostrov near Pieštany, Southwest Slovakia (Tirjaková 1988, p. 500); soil samples of the river side zone of the Danube river in Slovakia (Tirjaková 1992, p. 77); bark and decaying wood mass of *Corylus avellana* (hazelnut) in the Zliechov area, Slovakia (Bartošová & Tirjaková 2008, p. 178); non-saline and saline (2.1%) soils about 150 km east of Riyadh, Saudi Arabia (Foissner et al. 2008a, p. 310); forest and grassland soils near Sheldrick waterfalls, Shimba Hills Nature Reserve, Kenya (Foissner 1999, p. 322); in eight out of 73 soils samples from Namibia, including sand dunes of the Central Namib Desert (Foissner et al. 2002a, p. 58a, 68); litter and roots under moss in an autochthonous pine forest near Adelaide, Australia (Blatterer & Foissner 1988, p. 8). Tirjaková (1997a, p. 52) found *C. filiformis* in a brook (Hájsky potok) in Slovakia, perhaps due to terrestrial influences, for example fallen leaves.

Food not known. Biomass of 10^6 specimens about 5 mg (Foissner 1987a, p. 123; 1998, p. 200).

Taxa not Considered in the Gonostomatidae and its Synonym Cladotrichidae

The following genera, included in the cladotrichids by Small & Lynn (1985; Table 4), have features more or less clearly indicating that they do not belong to the Gonostomatidae, but to other higher taxa, for example, the amphisiellids (Berger 2008).

***Engelmanniella* Foissner, 1982**, Arch. Protistenk., 126: 66. Type species (by original designation): *Uroleptus mobilis* Engelmann, 1862. Remarks: Assigned to the Kahliellidae in the present review (p. 498).

***Lamtostyla* Buitkamp, 1977**, Acta Protozool., 16: 270. Type species (by original designation): *Lamtostyla lamottei* Buitkamp, 1977. Remarks: The cell division of the type species is not yet known. Thus, the classification of *Lamtostyla* in the Amphisiellidae is not quite certain (Berger 2008, p. 161).

***Perisincirra* Jankowski, 1978**, Tezisy Dokl. zool. Inst. Akad. Nauk. SSSR, year 1978: 40. Type species (by original designation): *Uroleptus kahli* Grolière, 1975. Remarks: At present assigned to the Kahliellidae (p. 463).

***Uroleptoides* Wenzel, 1953**, Arch. Protistenk., 99: 107. Type species (by original designation): *Uroleptoides kihni* Wenzel, 1953. Remarks: *Uroleptoides* is not very well defined because the type species is not described in detail. At present classified in the Amphisiellidae (Berger 2008, p. 224).

Kahliellidae Tuffrau, 1979

1979 **Kahliellidae n. fam.**[1] – Tuffrau, Trans. Am. microsc. Soc., 98: 525 (original description; Table 5). Name-bearing type genus: *Kahliella* Corliss, 1960.
1987 **Kahliellidae Tuffrau, 1979** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (classification of hypotrichs; Table 6).
1994 **Kahliellidae Tuffrau, 1979** – Tuffrau & Fleury, Traite de Zoologie, 2: 137 (revision of hypotrichs; Table 7).
1995 **Kahliellidae Tuffrau, 1979**[2] – Eigner, Europ. J. Protistol., 31: 363 (redefinition; Table 8).
1997 **Parakahliellidae n. fam.**[3] – Eigner, J. Euk. Microbiol., 44: 563 (original description; Table 13). Name-bearing type genus: *Parakahliella* Berger, Foissner & Adam, 1985.
1999 **Parakahliellidae** – Eigner, Europ. J. Protistol., 35: 46 (phylogenetic tree; Table 13).
1999 **Kahliellidae Tuffrau, 1979** – Shi, Song & Shi, Progress in Protozoology, p. 98 (revision of hypotrichs; Table 9).
2001 **Parakahliellidae** – Eigner, J. Euk. Microbiol., 48: 72 (comparison with the Orthoamphisiellidae, the Urostylidae, and the Oxytrichidae).
2001 **Kahliellidae Tuffrau, 1997** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 109 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).
2001 **Parakahliellidae Eigner, 1997** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 111 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).
2002 **Kahliellidae Tuffrau, 1979**[4] – Lynn & Small, Ciliophora, p. 454 (guide to ciliate genera; Table 10).
2007 **Kahliellidae Tuffrau, 1979** – Jankowski, Phylum Ciliophora, p. 461 (revision of ciliates; Table 11).
2008 **Kahliellidae Tuffrau, 1979** – Lynn, The ciliated protozoa, p. 357 (revision of ciliates; Table 12).

Nomenclature: The name Kahliellidae is based on the genus-group name *Kahliella* Corliss, 1960, while the name Parakahliellidae is based on *Parakahliella* Berger et al., 1985. Note that, as explained in chapter 7.2 of the general section (p. 41), the "defined endings" tagging the categories (e.g., family, subfamily) have no meaning in the present book.

Characterisation (A = supposed apomorphy): Dorsomarginalia[5]. Frontoventral cirri pattern relatively variable, originates primarily from six (I–VI) anlagen. Transverse cirri present or lost. One or more right and one or more left marginal rows. Pa-

[1] Tuffrau (1979) provided the following diagnosis: Formes essentiellement caractérisées par l'absence de cirres transverses et l'alignement longitudinal des rangées somatiques fronto-ventrales. Rangées marginales plus ou moins distinctes. Cirres frontaux parfois bien développés.
[2] Eigner (1995) provided the following redefinition: Euhypotrichina with more than one longitudinal cirral row on right side of body. Neokinetal anlagen develop during morphogenesis.
[3] Eigner (1997) provided the following diagnosis: The two rightmost ventral cirral rows for proter and opisthe are generated by the neokinetal 1 (N1) anlagen development. Dorsomarginal kineties present. Transverse cirri usually present. Old (parental) cilia and cirri may be present in interphase.
[4] Lynn & Small (2002) provided the following characterisation: At least two, typically more than two, ventral files, often not distinctly different from marginal cirral files; ventral cirral files may be preserved through variable number of cell divisions before being resorbed and replaced through additional new (= neokinetal) anlagen.
[5] The dorsal kinety pattern of the type species (*Kahliella acrobates*) of the name-bearing type genus is not described after protargol impregnation. Thus, it is not unequivocally known whether or not a dorsomarginal kinety is present. The very similar (perhaps synonymous) *K. simplex* has a dorsomarginal kinety indicating that the kahliellids are Dorsomarginalia.

rental frontoventral and/or marginal rows and/or dorsal kineties may be preserved through a variable number of divisions (A?). Dorsal kineties originate intrakinetally and dorsomarginally (not confirmed for all genera). Dorsal kinety fragmentation lacking. Caudal cirri present or lost.

The ground pattern of the Kahliellidae: For the Urostyloidea, the Amphisiellidae, the Trachelostylidae, the Gonostomatidae (p. 51), and the Hypotricha I discussed the ground pattern (Berger 2006a, 2008). Briefly, the ground pattern of a monophylum (evolutionary unit) is the combination of features of the stem-species from which the monophylum evolved, that is, it is a summary of apomorphies and more ore less young plesiomorphies (e.g., Ax 1995, Wägele 2001); old plesiomorphies, for example, the presence of cilia in the Kahliellidae, are usually not included in the ground pattern.

Unfortunately, I did not find a good apomorphy for the Kahliellidae, indicating that this group is non-monophyletic. The features generally used to characterise the kahliellids are not convincing.

Transverse cirri lacking. Transverse cirri are an old feature already present in the last common ancestor of the Hypotricha (Berger 2008). Probably, they evolved very early in the spirotrichs because they are present in the euplotids, a group branching off rather basally in the spirotrich tree. Further, the loss of a cirral group, including the transverse cirri, occurred very likely several times independently. But if the loss of the transverse cirri is indeed an apomorphy of the kahliellids, then *Fragmocirrus* branched off rather early because not yet all transverse cirri have been lost (Fig. 80f, h).

Parental cirri and/or dorsal bristles preserved in postdividers. At the first glance this feature is very impressive because it yields rows with widely (parental) or very widely (grandparental) spaced cirri (e.g., Fig. 65f). However, it is well documented that the preservation of parental cirri, which is a rather simple feature, evolved at least two times independently. In *Coniculostomum monilata*, a stylonychine oxytrichid according to my concept, parental right marginal cirri are displaced left of the new right marginal row causing a seemingly complicated pattern somewhat distracting from the close relationship of *Coniculostomum* with species of the *Stylonychia mytilus*-complex (Kamra & Sapra 1990; for review, see Berger 1999, p. 608). By contrast, Eigner (1995, 1997, 1999) assigned *Coniculostomum* to the Kahliellidae and Parakahliellidae, respectively, while he classified *Stylonychia mytilus* in the Oxytrichidae. In *Engelmanniella* the parental marginal cirri are arranged left of the new right and the new left marginal row (e.g., Fig. 87c–f). In *Kahliella simplex* the parental and grandparental frontoventral row VI are arranged right of the new frontoventral row VI, and the old left marginal rows are displaced left of the new left marginal row (Fig. 65f, g, 70g–k). In *Neogeneia hortualis* each left marginal row is composed of new and parental cirri (Fig. 84j–m), while in *Parakahliella* some parental dorsal kineties are retained in postdividers (Fig. 73n, 75o, r). The different patterns indicate that the preservation of old cirri and/or dorsal kineties is not an apomorphy of a single group, the kahliellids, but very likely evolved several times

independently. The convergent evolution of a much more complex "midventral pattern" indicates that within the hypotrichs convergencies are a rather common phenomenon (Foissner et al. 2004, Berger 2006a, Foissner & Stoeck 2008, Lynn 2008).

Longitudinal cirral rows. The species included in the kahliellids have, in addition to the two ordinary marginal rows, one or more longitudinal cirral rows, one or more of which are composed of old cirri in some species. According to Eigner (1995), the kahliellids have more than one longitudinal row right of the adoral zone. This is somewhat imprecise because many amphisiellids also have two long rows right of the adoral zone. However, in this group the so-called amphisiellid median cirral row is composed of cirri originating from two or three anlagen[1] while in the kahliellids all rows are formed from a single anlage. Of course there exist several other groups (e.g., urostyloids, *Stichotricha*; Berger 2006a, Foissner et al. 1991) which have more than two true cirral rows in the right body half, indicating that this feature is not very specific at that level.

Frontal cirri well developed. More or less well developed (enlarged) frontal cirri are already present in the last common ancestor of the Hypotricha (Berger 2008, p. 34). Thus, this feature is not usable as apomorphy of the kahliellids.

Neokinetal anlagen development. Eigner (1995, p. 342) introduced this term for a feature which occurs in five versions. Somewhat later, this concept was subtilised (Eigner 1997, 1999; see remarks below for some details). The composition of the taxa resulting from this concept is, however, very inhomogeneous according to morphological, ontogenetic, and molecular data, indicating that the features used are inadequate at the applied level.

Remarks: Tuffrau (1979) established the Kahliellidae primarily for hypotrichs which (i) lack transverse cirri, and which have (ii) longitudinal rows of frontoventral cirri, (iii) more or less distinct marginal rows, and (iv) well developed frontal cirri. Since then the Kahliellidae are a widely accepted group although the various characterisations (including mine) are rather vague (Tables 5–12).

Eigner (1995), who studied the cell division of *Kahliella simplex* (a very close relative or perhaps even a synonym of the type species *K. acrobates*), accepted the kahliellids. Somewhat later, however, he submerged the Kahliellidae in the Oxytrichidae because they share the so-called neokinetal 3 anlagen development (Eigner 1995, 1997), a rather vague feature[2]. However, neokinetal 3 is the plesiomorphic state of neokinetal anlagen development according to Fig. 2 in Eigner (1997). The two apomorphies characterising the oxytrichids sensu Eigner (1997; his Fig. 2) are the absence of parental cirri during interphase and the presence of transverse cirri. Unfortunately, *Kahliella* (an oxytrichid according to Eigner 1997, his Fig. 3) is the paragon for a hypotrich with parental cirri and, as emphasised by Tuffrau (1979), the kahliellids lack transverse cirri. Thus, the argumentation by Eigner (1997) is diffi-

[1] The amphisiellid median cirral row is therefore a mixed row according to Berger (2008, p. 2).

[2] According to Eigner (1997, p. 555) neokinetal 3 (N3) anlagen development is defined as follows: N3 designates the process by which one large usually V-shaped anlage generates four cirral rows for proter and opisthe's two rightmost ventral rows. The anlage develops mainly from cirri in the second ventral cirral row from right by long primary primordia, which later splits horizontally.

cult to follow. Interestingly, his "hypothesis" is seemingly supported by molecular data on a so far undescribed *Kahliella* species which clusters with *Halteria grandinella* and *Oxytricha granulifera*, type of *Oxytricha* and the oxytrichids (Gao et al. 2009, Kim et al. 2010). Supposed that the generic assignment of the undescribed *Kahliella* species is correct, a dorsomarginal row is present, but a kinety 3 fragmentation is lacking. The molecular placement is of course difficult to square with my concept that the oxytrichids are mainly characterised by a fragmentation of dorsal kinety 3. Supposed that the molecular assignment of *Kahliella* is correct, we would have to assume that the fragmentation was lost in the last common ancestor of the genus *Kahliella*. On the other hand the molecular analyses by Gao et al. (2009) and Kim et al. (2010) should not be overinterpreted because these papers mainly deal with oligotrichs, that is, the number of hypotrichs included in the analyses is very limited usually resulting in lame cladograms.

Kahliella is the name-bearing type genus and therefore *K. acrobates* the type of the whole group. Unfortunately, this species is not described in great detail, especially it is not known whether or not it has a dorsomarginal kinety. The very similar, perhaps even synonymous *K. simplex* has unequivocally a dorsomarginal row (Berger & Foissner 1987, Eigner 1995; p. 367), showing that *Kahliella* and the kahliellids belong to the Dorsomarginalia, a large subgroup of the hypotrichs comprising, inter alia, the oxytrichids and the uroleptids. The cyst of *Kahliella simplex* is basically of the *Oxytricha*-type because it has a four-layered cyst wall (Foissner & Foissner 1987). Perhaps this cyst-type is characteristic for the Dorsomarginalia. A dorsal kinety fragmentation is lacking in *Kahliella*, indicating that it is not very closely related to the oxytrichids, which have the fragmentation of kinety 3 as main morphological and morphogenetic apomorphy (Fig. 9a in Berger 2008). Note that some genera assigned to the oxytrichids in the first volume of the monograph (Berger 1999) are very likely misplaced in this group because they lack this characteristic feature, for example, *Urosoma*, *Urosomoida*, and some *Oxytricha* species (e.g., *Oxytricha lanceolata*). Since their final position is not yet certain, I preliminary classify them in the paraphyletic melting pot non-oxytrichid Dorsomarginalia (Berger 2008, p. 46).

As already mentioned above, Eigner (1997) synonymised the Kahliellidae with the Oxytrichidae. Simultaneously he established the Parakahliellidae for hypotrichs which produce the two rightmost frontoventral rows by the neokinetal 1 (N1) anlagen development. In addition, all have a dorsomarginal kinety, transverse cirri are usually present (interestingly, the name-bearing type genus *Parakahliella* lacks transverse cirri), and parental cirri may be present in postdividers. Most species previously assigned to the Kahliellidae by Eigner (1995) have been transferred to the parakahliellids. Since Eigner's concept is rather complicated, its original definition is given. According to Eigner (1997, p. 555), "N1 anlagen development designates the process by which two small usually V-shaped anlagen-parts generate each at least two cirral rows for proter and opisthe's two rightmost ventral rows; the posterior anlagen-part for the opisthe develops from cirri of the second ventral cirral row

from right; the anterior anlagen-part for the proter develops in four positions, viz. (1) also from cirri of the second ventral row from right (*Parakahliella macrostoma*, *Parentocirrus hortualis*, *Amphisiellides illuvialis*), (2) from cirri of the third ventral row from right (*Kerona polyporum*, *Clara vorax*, *C. pustulata*), (3) from cirri of the rightmost ventral row (*Paraurostyla weissei*), but mostly (4) de novo, above the posterior anlagen-part (*Onychodromus quadricornutus*, *Gastrostyla steinii*, *Onychodromus grandis*, *Coniculostomum monilata*, *Pattersoniella vitiphila*, *Histriculus muscorum*, *Steinia sphagnicola*, *Cyrtohymena muscorum*)." The high diversity of this feature strongly indicates that the phylogenetic analysis using this attribute cannot work. And indeed, the species originally included in the Parakahliellidae are now clearly assigned to rather different higher taxa, both according to classical analyses and molecular data (for details see chapter "Taxa excluded ..."; p. 545). The phylogenetic trees constructed by Eigner (1997, 1999) comprise 42 species, but only six features. Consequently, they are only very weekly resolved.

The Parakahliellidae have not been accepted in later revisions, whatever the reasons are (e.g., Lynn & Small 2002, Jankowski 2007, Lynn 2008). At present I also do not use this unambiguously overcrowded taxon, but I am sure that it can be reactivated in a slimed form when molecular data of much more "kahliellids" are available. Perhaps some very similar and therefore very likely closely related terrestrial genera (*Parakahliella*, *Afrokahliella*, *Fragmocirrus*) can be aggregated under the name Parakahliellidae

The designation of the cirral rows in the Kahliellidae is rather variable. For example, Berger & Foissner (1987) designated the rows with 1 to 11 in *Kahliella simplex*, starting with the outermost left marginal row. Eigner (1995) distinguished between the rows left and right of the adoral zone, and in addition, between new and parental rows. At the first glance the cirral pattern of several kahliellids is rather complex, mainly due to the preservation of cirri over one, two, or more generations. However, there is little doubt that the kahliellids have taken over several main features of the ground pattern of the Hypotricha, inter alia, the left and right marginal row and the frontoventral rows originating from the ordinary six (I–VI) anlagen. Thus, the rows are designated as marginal rows or as frontoventral rows I–VI. Only in few cases this designation is difficult to apply, for example in *Parakahliella*. *Parakahliella macrostoma* lacks one of these rows (likely V or VI), whereas in *P. haideri* dividers with a total number of five, six, or seven anlagen have been seen (e.g., Fig. 75q). To overcome this terminological problem, these "long" frontoventral rows are designated by their position (left and right) as already proposed by Foissner (1982). When more than two long rows are present, then they are named in detail (e.g., second from left) and designated in the illustration. Note that the dorsal kineties 1–3 and 5 of *Parakahliella* are homologous to kineties 1–3 and 4 of *Afrokahliella* and *Fragmocirrus* because in these two genera no parental kinety is retained after division.

The outermost left cirral row of *Kahliella* is composed of dorsal bristles (anterior portion) and cirri (posterior portion). I designate this combined row (term introduced

by Eigner 1995, p. 343) as dorsal kinety 1 because it divides in exactly the same manner and synchronous with the other dorsal kineties (Fig. 70g, h). The cirri of kinety 1 are therefore designated as caudal cirri.

Genera included in the Kahliellidae: *Kahliella* Corliss, 1960 (type genus); *Parakahliella* Berger, Foissner & Adam, 1985; *Afrokahliella* gen. nov.; *Fragmocirrus* Foissner, 2000; *Perisincirra* Jankowski, 1978; *Neogeneia* Eigner, 1995; *Engelmanniella* Foissner, 1982.

Kahliella is the name-bearing type genus of the Kahliellidae and therefore its inclusion needs no explanation. However, the question is whether or not the following genera are indeed closely related to *Kahliella* because no convincing unifying feature is known.

Parakahliella was originally classified in the kahliellids (Berger et al. 1985) and later fixed as name-bearing type of the parakahliellids by Eigner (1997). It lacks transverse cirri, has several longitudinal cirral rows, parental cirral rows and dorsal kineties are retained in the postdivider, and a dorsomarginal kinety is present. Thus, it is included in the kahliellids.

Afrokahliella comprises three "*Parakahliella*"-species almost exclusively known from Africa at present. Since they differ significantly in the dorsal morphogenesis from the remaining *Parakahliella*-species, which are perhaps confined to Eurasia, they are pooled to an own taxon.

Fragmocirrus with *F. espeletiae* as single species is from the Andean Páramo and differs from *Parakahliella* and *Afrokahliella* by the presence of (inconspicuous) transverse cirri. Originally classified in the parakahliellids by Foissner (2000).

Perisincirra is a difficult genus because the type species is not known in detail. Previously, *Perisincirra* was a melting pot for usually very slender, soil-dwelling species (e.g., Foissner 1982, Hemberger 1982). However, somewhat later most of which have been transferred to *Hemisincirra* Hemberger, 1985 (for review, see Berger 2008, p. 387). The remaining three species are mainly characterised by the widely spaced cirri within the individual rows. Since the dorsal kinety pattern and its formation are not known in detail for the type species *Uroleptus kahli* Grolière, 1975, the inclusion of *Perisincirra* in the kahliellids is uncertain; further, parental cirri are not preserved.

Neogeneia is a difficult genus because the type species lacks a non-ambiguous dorsomarginal kinety. The second species included is little known and therefore its assignment to *Neogeneia* is only a pragmatic one.

Engelmanniella with *Uroleptus mobilis* as single species is a well known taxon. In spite of that its phylogenetic position is difficult to estimate, inasmuch as the numerous molecular trees propose rather different positions. In the present book, *Engelmanniella* is assigned to the kahliellids because parental marginal rows are retained in postdividers. However, this assignment is only provisionally because a dorsomarginal row, present in *Kahliella*, is lacking in *Engelmanniella*.

Key to the genera included in the Kahliellidae: Since the kahliellids are an ill-defined group, no separate key is provided. Use the key on page 45.

Kahliella Corliss, 1960

1932 ***Kahlia acrobates* nov. gen., nov. sp.**[1] – Horváth, Arch. Protistenk., 77: 424, 432 (original description; see nomenclature for explanation of homonymy). Type species (by monotypy): *Kahlia acrobates* Horváth, 1932.

1932 ***Kahlia* J. Horvath, 1932** – Kahl, Tierwelt Dtl., 25: 546 (revision).

1934 ***Kahlia* Horwart** – Grandori & Grandori, Boll. Lab. Zool. agr. Bachic. R. Ist. sup. agr. Milano, 5: 281 (incorrect spelling of Horváth; guide to terrestrial protozoa).

1953 ***Kahlia* Horvath (1932)** – Jírovec, Wenig, Fott, Bartoš, Weiser & Šrámek-Hušek, Protozoologie, p. 510 (classification of protozoa).

1960 ***Kahliella* n. nom.** – Corliss, J. Protozool., 7: 275 (replacement name for *Kahlia* Horváth, 1932). Type species (same as for *Kahlia* Horváth, 1932, that is, by monotypy [see Article 67.8 of the ICZN 1999]): *Kahlia acrobates* Horváth, 1932.

1961 ***Kahliella* Corl.** – Corliss, Ciliated protozoa, p. 170 (revision of ciliates).

1961 ***Kahlia* Horwath** – Fauré-Fremiet, C. r. hebd. Séanc. Acad. Sci., 252: 3517 (classification of hypotrichs; incorrect spelling of Horváth).

1972 ***Kahliella* Corliss, 1960**[2] – Borror, J. Protozool., 19: 9 (revision of hypotrichs).

1974 ***Kahliella* (Horváth, 1932) Corliss, 1960** – Stiller, Annls hist.-nat. Mus. natn. hung., 66: 130 (notes on classification of hypotrichs; see nomenclature).

1974 ***Kahliella* Corliss** – Stiller, Fauna Hung., 115: 35 (guide to Hungarian ciliates).

1979 ***Kahliella* Corliss, 1960** – Tuffrau, Trans. Am. microsc. Soc., 98: 525 (classification of hypotrichs; establishment of the Kahliellidae).

1979 ***Kahliella* Corliss, 1960** – Corliss, Ciliated protozoa, p. 308 (revision of ciliates).

1979 ***Kahliella*** – Borror, J. Protozool., 26: 546 (exclusion from Urostylidae).

1979 ***Kahliella* Corliss, 1960** – Jankowski, Trudy zool. Inst., 86: 56 (generic catalogue of hypotrichs).

1982 ***Kahliella* Corliss, 1960** [3] – Hemberger, Dissertation, p. 27 (revision of hypotrichs).

1983 ***Kahliella* Corliss, 1960** – Curds, Gates & Roberts, British and other freshwater ciliated protozoa, p. 376 (guide to freshwater genera).

1985 ***Kahliella*** – Small & Lynn, Phylum Ciliophora, p. 458 (guide to ciliate genera).

1986 ***Kahliella* Corliss, 1960** – Dragesco & Dragesco-Kernéis, Faune tropicale, 26: 427 (guide to African species).

1987 ***Kahliella* Corliss, 1960** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (classification of hypotrichs).

1994 ***Kahliella*** – Corliss, Acta Protozool., 33: 15 (classification and characterisation of protists).

1994 ***Kahliella* Corliss, 1960** – Tuffrau & Fleury, Traite de Zoologie, 2: 137 (classification of hypotrichs).

1995 ***Kahliella* (Horváth, 1932) Corliss, 1960**[4] – Eigner, Europ. J. Protistol., 31: 363 (see nomenclature; improved diagnosis; redefinition of the Kahliellidae).

1999 ***Kahliella* Gorliss, 1960** – Shi, Song & Shi, Progress in protozoology, p. 99 (revision of hypotrichs; incorrect spelling of Corliss).

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[1] For the diagnosis of *Kahlia* provided by Horváth (1932), see *Kahliella acrobates*.

[2] Borror (1972) provided the following diagnosis: Cirri in 7–10 ventral rows. Apparently no transverse cirri. Two macronuclei.

[3] Hemberger (1982) provided the following diagnosis: Cirren in mehreren (7–10) ventralen Reihen; keine (oder kaum wahrnehmbare?, Verf.) morphologisch differenzierte Frontalcirren; keine Transversalcirren; Cirrenentwicklung aus longitudinalen Anlagen, hiernach lassen sich die uniform erscheinenden Cirren morphogenetisch differenzieren.

[4] Eigner (1995) provided the following improved diagnosis: More than one long cirral row on right and left side of body. At least three of them are typically parental (old) on each side (distinctly shorter than a neighboring cirral row and they usually contain wider spaced and enlarged cirri). Dorsomarginal kinety and combined cirral row. Neokinetal wave to the right on right side and to the left on left side of adoral zone of membranelles.

1999 ***Kahliella* Gorliss, 1960** – Shi, Acta Zootax. sinica, 24: 251 (revision of hypotrichs; incorrect spelling of Corliss).
2001 ***Kahliella* Corliss 1960** – Aescht, Denisia, 1: 86 (catalogue of generic names of ciliates).
2001 ***Kahliella* Corliss, 1960** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 41 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Kahliella* Corliss, 1960** [1] – Lynn & Small, Phylum Ciliophora, p. 455 (guide to ciliate genera).
2006 ***Kahliella* Corliss, 1960** – Berger, Monographiae biol., 85: 1210 (brief note on exclusion from urostyloids).
2007 ***Kahliella* Corliss, 1960** – Jankowski, Phylum Ciliophora, p. 461 (generic revision of ciliates).
2008 ***Kahliella* Corliss, 1960** – Berger, Monographiae biol., 88: 468 (brief note on exclusion from amphisiellids).
2008 ***Kahliella* Corliss, 1960** – Lynn, Ciliated protozoa, p. 357 (revision of ciliates).

Nomenclature: No derivation of the name *Kahlia* is given in the original description (Horváth 1932). Obviously, Horváth dedicated this genus to Alfred Kahl – the great German ciliatologist – because he studied and described *K. acrobates* in the city of Hamburg (Germany), where Kahl lived and worked. Corliss (1960, 1960a) found that *Kahlia* Horváth, 1932 is a junior homonym of *Kahlia* Ashmead, 1900, a hymenopteran dedicated to Hugo Kahl (Ashmead 1900, p. 107). Thus, Corliss (1960) introduced the replacement name *Kahliella*, which is a composite of *Kahlia* and the diminutive suffix *-ella*. Because of this ending, *Kahliella* is feminine (ICZN 1999, Article 30.1.3). *Kahliella* Corliss, 1960 is the name-bearing type of the Kahliellidae Tuffrau, 1979. Horváth (1932) did not specify the gender of *Kahlia*. Since the name ends in *-a*, it is to be treated as feminine (ICZN 1999, Article 30.2.4).

Ashmead (1900) fixed the type species of *Kahlia* (a junior synonym of *Phaenocarpa* Förster) as follows: "Type, *Kahlia flavipes* Ashmead, manuscript". At present I do not know whether the type species *K. flavipes* was ever published validly. However, genera established before 1931 are even valid when no type species was fixed (ICZN 1999, Article 67.4.1), and therefore *Kahlia* Horváth, 1932 is in any case the junior homonym and its replacement by *Kahliella* was valid. Incorrect subsequent spellings of *Kahlia* and *Kahliella*: *Kakliella acrobates* (Olins & Olins 1994, p. 150); *Kalia acrobates* (McCashland 1956, p. 38).

Kahliela Tucolesco, 1962 is not a junior homonym of *Kahliella* Corliss, 1960 because of one-letter difference (ICZN 1999, Article 56.2). It cannot be interpreted as incorrect original spelling because Tucolesco (1962) mentioned the name only once and he did not provide a derivation of the name. Further, Tucolesco (1965, p. 162) also wrote *Kahliela*, proving that this spelling was intended.

The type fixation in *Kahlia* Horváth, 1932 is by monotypy because the fixation by the expression "nov. gen., nov. spec." is interpreted as original designation only for papers which have been published before 1931 (ICZN 1999, Article 68.2.1).

[1] Lynn & Small (2002) provided the following characterisation: More than five midventral cirral files extending well past cell equator; cirri not densely packed; oral cavity restricted to anterior one-third of cell; transverse cirri, absent; caudal cirri, absent.

The authorship in Stiller's (1974a) and Eigner's (1995) entry in the list of synonyms is incorrect because in genera only the author (Corliss) of the replacement name is given; the author (Horváth) of the preoccupied name is ignored.

Dragesco (1970, p. 98) introduced the name *Plesiotricha*. However, since it was proposed only conditionally and published after 1960 it is not available (ICZN 1999, Article 15.1; Aescht 2001, p. 128). Consequently, it cannot be a synonym of *Kahliella* as proposed by Shi (1999) and Shi et al. (1999). In spite of that, the etymology is explained: *Plesiotricha* is a composite of the Greek *plesi-* (near, neighbouring; primitive), the thematic vowel *·o-* (at the end of the first root when the second begins with a consonant), the Greek noun *trich-* (hair, cilia), and the inflectional ending *-a*. According to Dragesco (1970), it refers to the "primitive" ("plesiomorphic" because composed of several, similar cirral rows) cirral pattern.

Characterisation (A = supposed apomorphy): Kahliellidae with adoral zone of membranelles and undulating membranes roughly in *Gonostomum*-pattern (A?). Three long frontoventral rows formed by anlagen IV, V, and VI. Old frontoventral rows VI shifted rightwards of new row VI (A). Left marginal rows of up to three generations retained left of newly formed left marginal row. Transverse cirri lacking. Three bipolar dorsal kineties; posterior half of leftmost kinety usually composed of cirri (A?); remaining bipolar kineties without caudal cirri; dorsomarginal kinety present (see remarks at *K. acrobates*); dorsal kinety fragmentation lacking. Mainly terrestrial.

Additional characters: According to present knowledge, the two species included differ only in the dorsal kinety pattern. Since the type species is not yet described after protargol impregnation it cannot be excluded that the two species are synonymous.

Remarks: Horváth (1932) established *Kahlia* because he recognised that his population cannot be assigned to a known genus. He classified it in the subfamily Urostylinae, which was characterised by a high number of cirri arranged in several rows at that time. Horváth (1932) put it "between" *Kerona* and *Urostyla* because *Kahlia acrobates* (type) has 10 cirral rows, a value which is in between those of *Kerona* (six rows) and *Urostyla* (more than 10 rows). This higher level classification, which is certainly incorrect, was taken over by Fauré-Fremiet (1961a) and Stiller (1974, p. 130). The misclassification is understandable because the urostyloids were insufficiently defined until that time due to the lack of details of the cirral pattern and its formation. Now we know that urostyloids are hypotrichs with (i) more than six frontal-ventral-transverse cirri anlagen forming cirral pairs primarily arranged in a zigzag pattern and (ii) bipolar dorsal kineties only, that is, dorsomarginal rows and a dorsal kinety fragmentation are lacking. For a recent review of this group, see Berger (2006a).

Tuffrau (1970, 1972) supposed a close relationship of *Kahliella* and *Hypotrichidium*. Somewhat later he established the Kahliellidae with *Kahliella* as name-bearing type genus (Tuffrau 1979). This classification was retained by Tuffrau (1987), Tuf-

frau & Fleury (1994), Shi (1999), Shi et al. (1999), Lynn & Small (2002), Jankowski (2007), and Lynn (2008), and is also used in the present review.

By contrast, Corliss (1977, p. 137; 1979) and Borror (1979, p. 548) assigned *Kahliella* to the Spirofilidae because transverse cirri are lacking and morphogenesis shows similarities with *Hypotrichidium*, the senior synonym of the name-bearing type *Spirofilum*. I strongly doubt a close relationship of *Kahliella* and *Hypotrichidium* because the cirral pattern of the euplanktonic *Hypotrichidium* (for review, see Foissner et al. 1999, p. 677) deviates distinctly from that of *Kahliella*, which lives in soil. In addition, *Hypotrichidium* lacks a dorsomarginal kinety whereas such a kinety is present in *K. simplex* (note that the lack of this kinety in the original description of *K. acrobates* was never confirmed!). Borror & Evans (1979, p. 55) debated a relationship with *Cladotricha*, a difficult genus because the type species is not known in detail (p. 235). *Cladotricha* species described with modern methods, for example *C. australis* (Fig. 48a–h), lack parental cirri and have a simple dorsal kinety pattern, that is, only three bipolar kineties.

Wicklow (1979) discussed that the ventral morphogenesis of *Kerona polyporum* (= *Kerona pediculus* in Berger 1999, p. 826) is reminiscent of that found in *Kahliella* because "six ventral rows of cirri arise in part as frontal streaks from the developing oral primordium in the opisthe and the differentiation of the paroral apparatus in the proter, and independently as streaks from the dedifferentiation of row 5 in the opisthe and row 4 in the proter". I suppose that this agreement is only a plesiomorphy and therefore not usable to elucidate the phylogenetic relationships. The different mode of dorsal morphogenesis (multiple fragmentation in *Kerona* vs. fragmentation lacking in *Kahliella*) strongly indicates rather different phylogenetic positions of these taxa. For review of *Kerona*, which very likely belongs to the oxytrichids, see Berger (1999, p. 825).

Hemberger (1982, p. 19) classified *Kahliella* in the Amphisiellidae because longitudinal cirri anlagen and ventral rows are present. However, *Kahliella* differs from the amphisiellids, inter alia, by the lack of the so-called amphisiellid median cirral row which is composed of cirri of two (V and VI) or three (IV–VI) anlagen (for review, see Berger 2008). In addition, amphisiellids lack a dorsomarginal kinety, which is present in *Kahliella simplex*. These morphological differences strongly indicate that *Kahliella* is not closely related to the amphisiellids. The classification in the Amphisiellidae was taken over by Small & Lynn (1985).

Recently, Kim et al. (2010) found in molecular analyses that an unidentified *Kahliella* species is closely related to *Halteria grandinella* and *Oxytricha granulifera*. By contrast, *Amphisiella* – as defined by Berger (2008) – usually branches off rather basally in the Hypotricha trees. A relationship of *K. simplex* and the oxytrichids was also proposed by Eigner (1997, p. 555) because a V-shaped cirral anlage is formed and primary primordia are present. However, the analyses by Kim et al. (2010) are based on only 12 hypotrichs so that the results should not be overinterpreted. In addition, the *Kahliella* species used is not yet described morphologically making a more detailed statement impossible. Shi (1993) assigned *Kahliella* to the

Rootletphorida, a higher taxon characterised, inter alia, by "left-ward transverse rootlet fiber in the marginal cirral base".

The previous paragraphs show that *Kahliella* was classified in six(!) higher taxa, namely, the Amphisiellidae, the Kahliellidae, the Oxytrichidae, the Rootletphorida, the Spirofilidae, and the Urostylidae. This high diversity of classifications impressively shows the uncertainty about its phylogenetic position. Provided that *Kahliella* has a dorsomarginal kinety (see remarks at *K. acrobates*) I suppose that it is a non-oxytrichid dorsomarginalian hypotrich (Berger 2008, p. 46) and classify it, like Tuffrau (1979), Tuffrau & Fleury (1994), Lynn & Small (2002), Jankowski (2007), and Lynn (2008), in the Kahliellidae. For a more detailed discussion of this topic, see same chapter at the Kahliellidae.

Shi et al. (1999) and Shi (1999) synonymised five genera with *Kahliella* Corliss, 1960, namely (i) *Uroleptopsis* Kahl, 1932; (ii) *Plesiotricha* Dragesco, 1970; (iii) *Pseudokahliella* Berger, Foissner & Adam, 1985; (iv) *Parakahliella* Berger, Foissner & Adam, 1985; and (v) *Neogeneia* Eigner, 1995. *Uroleptopsis* is a pseudokeronopsid, that is, a hypotrich with a urostyloid midventral complex and a macronucleus whose many nodules do not fuse to a single mass during cell division (Berger 2004; 2006a, p. 980). Consequently, a synonymy of *Kahliella* and *Uroleptopsis* is almost impossible. I suppose that Shi and co-workers synonymised *Uroleptopsis* with *Kahliella* simply because *Uroleptopsis multiseta* Dragesco, 1970 is a junior synonym of *K. acrobates* (see there). *Plesiotricha* is a name which is nomenclaturally not available and thus it cannot be a synonym (see nomenclature). *Pseudokahliella* was established for *Kahliella marina* Foissner, Adam & Foissner, 1982 (p. 662), which is marine and, inter alia, lacks a dorsomarginal kinety. By contrast, *Kahliella* is terrestrial and has such a kinety. Interestingly, the synonymy was reversed by the Chinese workers themselves in that they again accepted *Pseudokahliella* (Hu & Song 2003). *Parakahliella* forms two or more new marginal rows per side (vs. one in *Kahliella*) and lacks the gonostomatid oral apparatus (vs. present in *Kahliella*), strongly indicating that the separation seems justified. In *Neogeneia* the left marginal rows are composed of a newly formed anterior portion and a parental posterior portion (Eigner 1995); in addition, it lacks a dorsomarginal kinety (p. 481). Both features indicate that both *Neogeneia* and *Kahliella* are valid.

Kahliella usually forms the frontal-ventral cirri via the plesiomorphic number of six anlagen, a feature obviously taken over from the ground pattern of the Hypotricha (Berger 2008). The cirral pattern in *Kahliella* is rather variable due to the preservation of parental, grandparental, and great-grandparental cirri.

A relatively high number of species was originally described in or transferred to *Kahliella*. However, the present review shows that basically only the two species described by Horváth (1932, 1934) remain in this genus. The other species have been transferred to a rather different number of genera. A major problem in *Kahliella* is, as already briefly mentioned above, that *K. acrobates* (type species) and *K. simplex* differ significantly in the dorsal kinety pattern. Interestingly, the pattern of the type species (without dorsomarginal kinety) was never confirmed. Thus, one cannot ex-

clude that these two species are synonymous, which would mean that *Kahliella* is monotypic at the present state of knowledge (details see *K. acrobates*).

Kahliella has an oral apparatus closely resembling that of *Gonostomum* (p. 58), that is, an adoral zone which commences anteriorly, extends laterally, and suddenly curves rightwards (Fig. 3a, 4a). The buccal field is narrow, the endoral relatively long, and the paroral rather short. However, the cilia of the paroral of *Kahliella* are not widely spaced as in *Gonostomum*. By contrast, the dorsal infraciliature differs significantly because in *K. simplex* a dorsomarginal kinety is present while this structure is lacking in *Gonostomum*. Thus, the kahliellids and the gonostomatids cannot be closely related according to the Dorsomarginalia-concept (Berger 2006a, p. 38). The clear separation is supported by the molecular analysis by Kim et al. (2010), but not by that of Gao et al. (2009). According to the sparse molecular data, *Kahliella* sp. is the sistergroup of the halteriids (e.g., *Halteria*, *Pelagohalteria*, *Meseres*[1]). Further comments on the studies by Gao et al. (2009) and Kim et al. (2010), see remarks at the Kahliellidae.

[1] Schewiakoff (1892, p. 560) described the two ciliate species "*Meseres cordiformis* n. g. et sp." and "*Meseres stentor* n. g. et sp.". According to Aescht (2001, p. 98), these are nomina nuda because no description or definition was provided. However, this is incorrect because Schewiakoff (1892) described both species more or less detailed (note that Aescht 2001, p. 288 also wrote "*Meseres* Schewiakoff 1892"). Thus, Schewiakoff (1892) is the author, and not Schewiakoff (1893, p. 62, 64, Tafel IV, Fig. 54–56), who described the species a second time (*Mesetes* in Schewiakoff 1893, p. 106 is an incorrect subsequent spelling). Unfortunately, neither Schewiakoff (1892) nor Schewiakoff (1893) fixed one of the two species as type. Since Schewiakoff (1892, 1893) applied the expression "n. g. et sp." to both species, Article 68.2.1 of the ICZN (1999) cannot be applied; other articles (e.g., 68.2.2 or 68.4) also do not pertain. Further, no later author has ever fixed a type species for *Meseres* Schewiakoff, 1892 (e.g., Kahl 1932, Petz & Foissner 1992, Aescht 2001). Only recently, Jankowski (2007, p. 501; note that Jankowski used – likely par lapsus – the incorrect year 1882) fixed *Meseres cordiformis* as type by subsequent designation (ICZN 1999, Article 69.1; note that a genus established before 1931 is valid even when no type species was fixed, Article 69). Simultaneously, Jankowski (2007, p. 502) established the genus *Petzinus* with *Meseres corlissi* Petz & Foissner, 1992 as type species: *Petzinus corlissi* (Petz & Foissner, 1992) Jankowski, 2007.

The second nomenclatural problem with *Meseres* is that just one year after Schewiakoff (1892), Ludwig (1893, p. 106, 107) described the homonymous, monotypical holothurid genus *Meseres* (Echinodermata) with *M. macdonaldi* as type species. According to Ludwig (1894, p. 5), who described and illustrated the species in detail (p. 34), a preliminary report was provided in the "Bulletin of the Museum of comparative Zoology" (Ludwig 1893) and in the "Zoologischer Anzeiger" (vol. 16, year 1893, No. 420, p. 177–186; I did not check this paper and therefore I do not know which of the two preliminary reports from 1893 is the "true" original description; according to the Nomenclator Zoologicus, vol. 3, p. 112, the Zoologische Anzeiger contains the original description). Anyhow, *Meseres* Ludwig, 1893 is the junior homonym of *Meseres* Schewiakoff, 1892 (Nomenclator Zoologicus, vol. 3, p. 112). According to O'Loughlin & Ahearn (2005, p. 150, 177), *Meseres* Ludwig is a valid, monotypic genus without synonym. Thus, for *Meseres* Ludwig, 1893 a new substitute name is introduced (ICZN 1999, Article 60): *Echinomeseres* nom. nov. Type species (same as for *Meseres* Ludwig, 1893): *Meseres macdonaldi* Ludwig, 1893 – *Echinomeseres macdonaldi* (Ludwig, 1893) comb. nov. Etymology: *Echinomeseres* is a composite of *ho echinos* (Greek, the hedgehog; Hentschel & Wagner 1996, p. 222; the first part of the name Echinodermata) and the genus-group name *Meseres* (Greek; means "standing in the middle" according to Schewiakoff 1893, p. 64, respectively, "standing between two parties" according to Ludwig 1894, p. 34). It shall simply indicate the higher level classification. Like *Meseres* masculine (Aescht 2001, p. 288). Species assignable: type species only according to O'Loughlin & Ahearn (2005, p. 177).

There exist several records of unidentified *Kahliella* species. Bovee (1960, p. 357) recorded a *Kahlia* sp. in an artificial farm pond in the Mountain Lake Region, Giles County, Virginia, USA. Later, he found a *Kahliella* sp. in the aufwuchs of the softshell turtle, *Trionyx muticus*, collected in the Kansas River near Lawrence, Kansas, USA (Bovee 1981, p. 100). Jayaramaraju & Kalavati (1986, p. 202) found a *Kahlia* in a freshwater lake in India, and Charubhun & Charubhun (2000, p. 491) recorded a *Kahlia* sp. in a freshwater habitat in Thailand.

Species included in *Kahliella* (alphabetically arranged basionyms are given): (1) *Kahlia acrobates* Horváth, 1932 (type species); (2) *Kahlia simplex* Horváth, 1934. Incertae sedis: (3) "New Genus" by Conn (1905).

Species misplaced in *Kahliella*: The following species – largely originally classified in *Kahliella* or *Kahlia* – are now assigned to other genera within the kahliellids, or they do not belong to the kahliellids at all. Synonyms of "true" *Kahliella* species are not mentioned in the following list. If you do not find a certain name in the list below, see the index.

Kahlia bacilliformis Gelei, 1954. Remarks: Now *Deviata bacilliformis* (p. 578).

Kahlia costata Kahl, 1932. Remarks: Now *Neogeneia costata* (p. 494).

Kahliella franzi (Foissner, 1982) Berger & Foissner, 1988. Remarks: Now type species of *Neowallackia* (p. 281).

Kahliella marina Foissner, Adam & Foissner, 1982. Remarks: Now *Pseudokahliella marina* (p. 663).

Kahliella quadrinucleata Dragesco, 2003. Remarks: Now *Deviata quadrinucleata* (p. 558).

Kahliella spirostoma Alekperov, 1988. Remarks: Now *Deviata spirostoma* (p. 597).

Kahliella zignis (Entz, 1884) Borror, 1972 (basionym: *Uroleptus zignis* Entz, 1884). Remarks: Now *Australothrix zignis* (Entz, 1884) Blatterer & Foissner, 1988. For review, see Berger (2006a, p. 721).

Psilotricha dragescoi Grolière, 1975, p. 482. Remarks: According to Hemberger (1982, p. 29), *Psilotricha dragescoi* could – especially as concerns body shape and cirral pattern – belong to *Kahliella*. However, the adoral zone almost forms a three-quarter circle indicating that a classification in *Kahliella* is as uncertain as the original classification, which is therefore preliminary accepted.

Key to *Kahliella* species and similar species

If you cannot identify your specimen/population with the key below, see also keys to *Wallackia* (p. 206) or *Gonostomum* (p . 58). Note that *K. acrobates* (type species) and *K. simplex* differ very likely only in the dorsal kinety pattern (dorsomarginal kinety absent vs. present), which is, however, not yet confirmed for *K. acrobates* in protargol preparations.

1 Two macronuclear nodules; rows with widely spaced cirri at both cell margins (e.g., Fig. 65a). . . . . *Kahliella acrobates*-group **2**
- More than 2 macronuclear nodules; rows with widely spaced cirri lacking (Fig. 52a, e, 72a). **3**

2 Four dorsal kineties, including a short dorsomarginal kinety (= kinety 4; Fig. 65g, o, 67f, 70c). . . . . *Kahliella simplex* (p. 367)
- Five dorsal kineties, short dorsomarginal kinety lacking (Fig. 62e). . . . . *Kahliella acrobates* (p. 354)

3 (1) 7–17, on average 12 macronuclear nodules (Fig. 52a–e). . . . . *Neowallackia franzi* (p. 281)
- Four macronuclear nodules (Fig. 72a). . . . . "New Genus" by Conn (1905), an uncertain taxon (p. 396)

Kahliella acrobates-group

The two *Kahliella* species differ basically only in the dorsal kinety pattern, a feature insufficiently known in the type species. Thus, if you are uncertain about this feature, write *K. acrobates*-group.

Kahliella acrobates (Horváth, 1932) Corliss, 1960
(Fig. 62a–m, 63a–d, 64a–l, Table 22)

1932 ***Kahlia acrobates* nov. gen., nov. sp.**[1] – Horváth, Arch. Protistenk., 77: 424, 432, Fig. 1A–C, 2–6 (Fig. 62a–i; original description; very likely no type material available, see nomenclature).

1932 ***Kahlia acrobates* J. Horvath** – Kahl, Tierwelt Dtl., 25: 546, Fig. 90 (Fig. 62j, k; revision).

1934 ***Kahlia acrobates* Horwart** – Grandori & Grandori, Boll. Lab. Zool. agr. Bachic. R. Ist. sup. agr. Milano, 5: 281, Fig. XXXIVA–C (redrawings of Fig. 62j, k; micrograph of resting cyst; incorrect spelling of Horváth).

1953 ***Kahlia acrobates*** – Jírovec, Wenig, Fott, Bartoš, Weiser & Šrámek-Hušek, Protozoologie, p. 509, Fig. 234D (redrawing of Fig. 62j; classification of protozoa).

1960 ***Kahliella acrobates* n. comb.** – Corliss, J. Protozool., 7: 275 (combination with *Kahliella*).

1963 ***Kahlia acrobates* Horvath** – Lundin & West, Free-living protozoa, p. 67, Plate 27, Fig. 4 (Fig. 62l; illustrated record).

1967 ***Kahlia acrobates* Kent** – Chardez, Revue Écol. Biol. Sol, 4: 294, Fig. 31 (Fig. 62m; illustrated record; incorrect author).

1969 ***Kahliella acrobates*** – Tuffrau, Protistologica, 5: 228, Planche I, Fig. 1–5, Fig. I–III, IV C (Fig. 64a–l; morphogenesis).

1970 ***Uroleptopsis multiseta* n. sp.** – Dragesco, Annls Fac. Sci. Univ. féd. Cameroun, Numéro hors-série: 97, Fig. 71, 72 (Fig. 63a, b; original description of synonym; no formal diagnosis provided; the ho-

[1] Horváth (1932) provided the following diagnosis: Der Körper ist gestreckt oval, metabolisch, farblos, nur die Nahrung verleiht ihm ein wenig Farbe. Es besitzt acht Bauchcirrenreihen, seine Randcirren sind an beiden Seiten in Rückencirren umgewandelt. Analcirren und Schwanzborsten fehlen. Stirncirren hat es vier, oft noch mehr und fünf Reihen dorsaler Tastborsten. Das Peristom ist kurz und schmal. Seine Bewegung ist ein schnelles Schwimmen mit einer Drehung nach rechts oder links, oder ein langsames Kriechen. Es lebt in stagnierendem Wasser. Seine Nahrung sind Bakterien, Algen und Ciliaten.

lotype slide [accession number 2002/918] is deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria, details see Aescht 2008, p. 167).

1972 ***Kahliella acrobates* (Horváth, 1932) Corliss, 1960** – Borror, J. Protozool., 19: 9 (revision of hypotrichs).

1982 ***Kahliella acrobates* (Horváth, 1932) Corliss, 1960** – Hemberger, Dissertation, p. 27 (revision of non-euplotid hypotrichs).

1986 ***Kahliella microstoma* n. sp.** – Dragesco & Dragesco-Kernéis, Faune Tropicale, 26: 429, Planche 125 A, B (Fig. 63c, d; replacement name for *Uroleptopsis multiseta*, see nomenclature).

2001 ***Kahliella acrobates* (Horváth, 1932) Corliss, 1960** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 40 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: No derivation of the species-group name *acrobates* is given in the original description. The name *acróbates* (*akrobatein*; Greek; to walk on tiptoe, daringly moving; Hentschel & Wagner 1996) possibly refers to the fast swimming. Type species of *Kahlia* Horváth, 1932 and *Kahliella* Corliss, 1960. No derivation of the species-group name *microstoma* is given by Dragesco & Dragesco-Kernéis (1986). It is a composite of the Greek adjective *micr-* (small, low), the thematic vowel *·o-* (at the end of the first root when the second begins with a consonant; Werner 1972), and the Greek noun *to stóma* (mouth) and refers to the relatively short adoral zone of membranelles. For derivation of the species-group name *multiseta*, see *Kahliella multiseta* Dragesco, 1970 at *K. simplex*.

Dragesco (1970) described the two new species *Uroleptopsis multiseta* (p. 97) and *Kahliella multiseta* (p. 105). Dragesco & Dragesco-Kernéis (1986, p. 429) transferred *Uroleptopsis multiseta* to *Kahliella* which thus became a secondary homonym – as *Kahliella multiseta* (Dragesco, 1970) Dragesco & Dragesco-Kernéis, 1986 – of *Kahliella multiseta* Dragesco, 1970. Consequently, they introduced a new species-group name ("*Kahliella microstoma* n. sp.") for *U. multiseta*. However, instead to use the correct term "nom. nov." (abbreviation for nomen novum; new name or replacement name or substitute name) they incorrectly established a new species. Anyhow, if someone considers this species as valid in the genus *Kahliella* it has to be cited as follows: *Kahliella microstoma* Dragesco & Dragesco-Kernéis, 1986. Foissner (1987b, p. 230) also discussed this nomenclatural problem. The confusing situation clearly shows that it is unwise to provide similar species with the same species-group name.

Dragesco (1970, p. 98) conditionally introduced the genus *Plesiotricha* for *Uroleptopsis multiseta* Dragesco, 1970. However, *Plesiotricha* is not available (see nomenclature of *Kahliella*). Thus, all combinations with this genus-group name are also not available, for example, "*Plesiotricha multiseta* Dragesco, 1970" in Borror (1972, p. 9), "*Plesiotricha multiseta* (Dragesco) Borror, 1972" in Dragesco & Dragesco-Kernéis (1986, p. 429), and "*Plesiotricha multiseta* (Dragesco, 1970) Dragesco, 1970" in Berger (2001, p. 97).

Incorrect subsequent spellings: *Kahliella acrobate* Corliss, 1960 (Hu & Song 2003, p. 2042; authorship also incorrect, see heading above); *Uroleptapsis multiseta* in Dragesco (1970, p. 98) and Dragesco & Dragesco-Kernéis (1986, p. 429) and *Uroletapsis multiseta* Dragesco, 1970 in Dragesco (1980, p. 181) are incorrect sub-

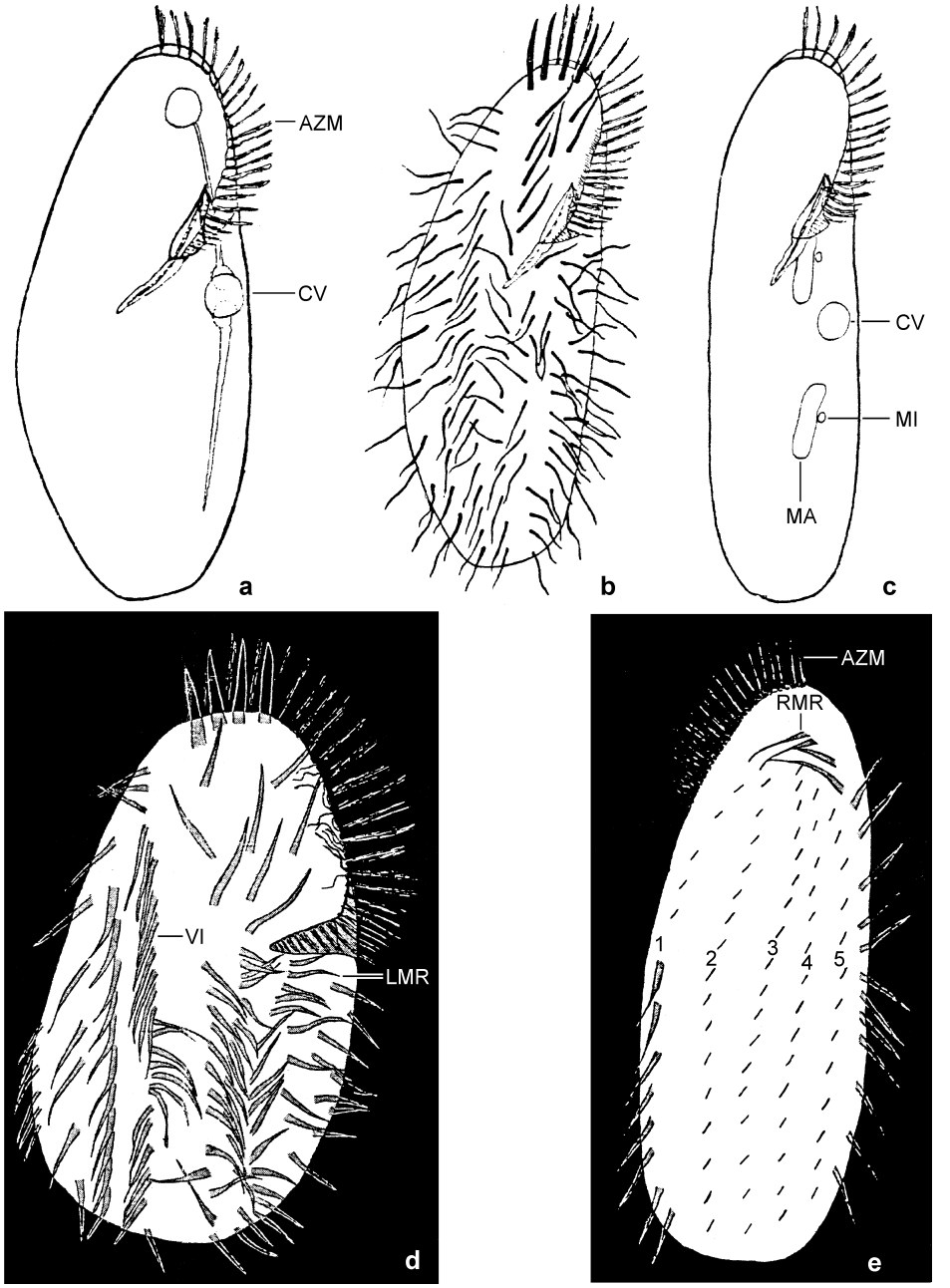

Fig. 62a–e *Kahliella acrobates* (from Horváth 1932. a–c, from life and after fixation and staining; no details given in the legend; d, e, opalblue stain). **a–c:** Ventral view of a postdivider (with parental contractile vacuole in frontal area), an interphasic specimen, and a specimen ready to divide (no sizes indicated). **d, e:** Infraciliature of ventral and dorsal side, about 125 µm. Details see text. AZM = adoral zone of membranelles, CV = contractile vacuole, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row, VI = frontoventral row VI, 1–5 = dorsal kineties. Page 354.

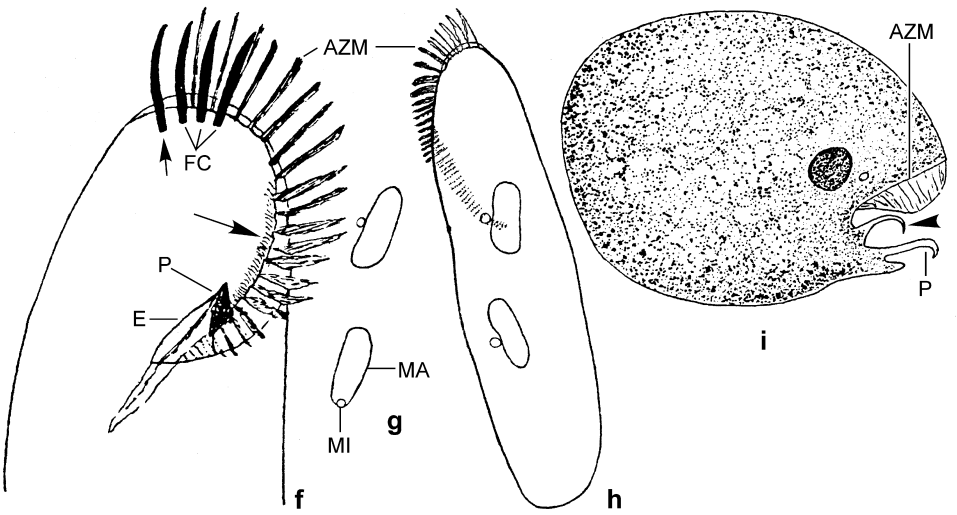

Fig. 62f–i *Kahliella acrobates* (from Horváth 1932. f, wet silver-nitrate impregnation; g, h, Feulgen stain; i, Haidenhain-hematoxylin stain). **f:** Oral apparatus; long arrow marks lateral membranellar cilia, short arrow denotes anteriormost cirrus of anlage IV or VI. **g, h:** Nuclear apparatus. **i:** Cross-section in oral area; arrowhead marks endoral. AZM = adoral zone of membranelles, E = endoral, FC = frontal cirri, MA = macronuclear nodule, MI = micronucleus, P = paroral. Page 354.

sequent spellings of *Uroleptopsis* Kahl, 1932, a urostyloid taxon (for review, see Berger 2006a, p. 980).

Horváth (1932, 1934) made various stains of *K. acrobates* and *K. simplex* (Fig. 62d, e, 67a–h). Thus, it cannot be excluded that permanent slides are still available somewhere in the University of Szeged (Hungary), where Horváth worked. I did not check the availability because it is extremely unlikely that usable slides are still present.

Remarks: The original description of *Kahliella acrobates* is rather detailed, but contains two uncertainties. The first concerns the type locality which is not clearly fixed; for details, see occurrence and ecology. The second uncertainty pertains the dorsal kinety pattern which is described and illustrated (Fig. 62e), but differs significantly from that of *K. simplex* (Fig. 65g, o, 66b, 67f), the second *Kahliella* species, which is indistinguishable from *K. acrobates* in all other features. The dorsal kinety pattern is a difficult feature in *Kahliella* because it shows, in contrast to most other hypotrichs, a relatively high variability (e.g., Fleury & Fryd-Versavel 1982). According to the original description, *Kahliella acrobates* has five dorsal kineties (Fig. 62e). The anterior half of kinety 1 is composed of bristles, the posterior one is made of caudal cirri. The remaining four kineties (kineties 2–5) are more or less of body length (Fig. 62e), indicating that *K. acrobates* lacks a dorsomarginal kinety because dorsomarginal rows are usually distinctly shortened posteriorly. *Kahliella simplex* has the same type of kinety 1 as *K. acrobates*, but only two kineties (kineties 2, 3) of

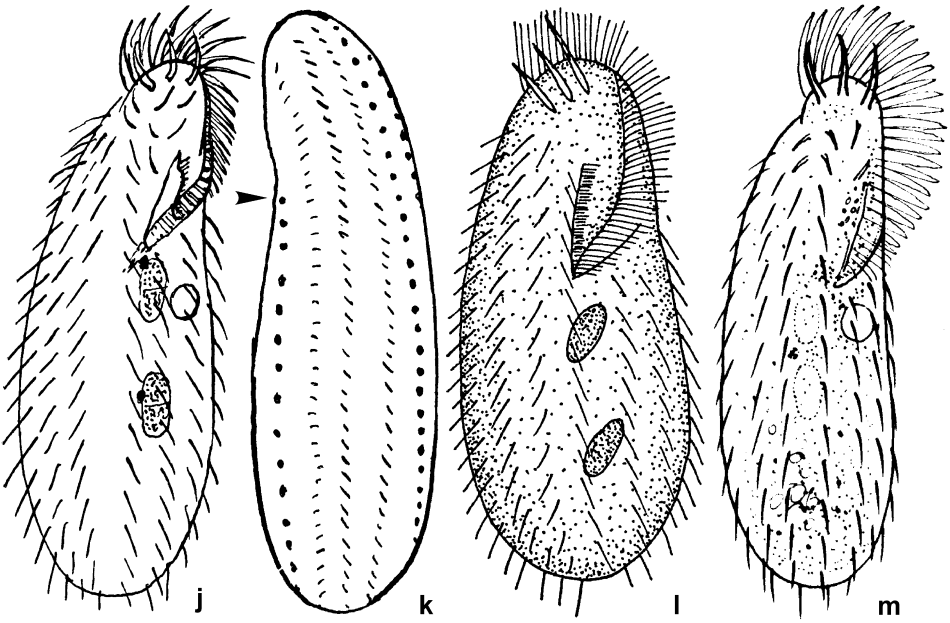

Fig. 62j–m *Kahliella acrobates* (j, k, from Kahl 1932; l, from Lundin & West 1963; m, from Chardez 1967. j–m, from life). Infraciliature of ventral (j, l, m) and dorsal side (k), j, k = 100–200 µm, l = size not indicated, m = 135 µm. Arrowhead in (k) marks anterior end of caudal cirri portion on dorsal kinety 1. Note that in all three populations three distinctly enlarged frontal cirri are illustrated. Page 354.

body length and one dorsomarginal kinety (kinety 4), which is distinctly shortened posteriorly (Fig. 65g, o, 67f, 70c). Unfortunately, no modern redescription confirming the original description of *K. acrobates* is available and very likely no type material exists (see nomenclature). Thus, it cannot be excluded that Horváth (1932) misinterpreted the dorsal infraciliature of *K. acrobates* because it is unlikely that *K. acrobates* and *K. simplex*, which basically have the same cirral pattern and occurred at the same locality (Horváth 1936, p. 482), differ so distinctly in the dorsal infraciliature. The main problem with the different dorsal kinety patterns is the dorsomarginal row, which is evidently lacking in *K. acrobates*, but certainly present in *K. simplex*. The presence of such a row is the main feature of the Dorsomarginalia Berger, 2006a. On the other hand, Horváth (1932) obviously recognised the cirral pattern of *K. acrobates* rather exactly so that the correctness of the dorsal kinety pattern cannot be doubted straight away. As a consequence of this unsatisfactory situa-

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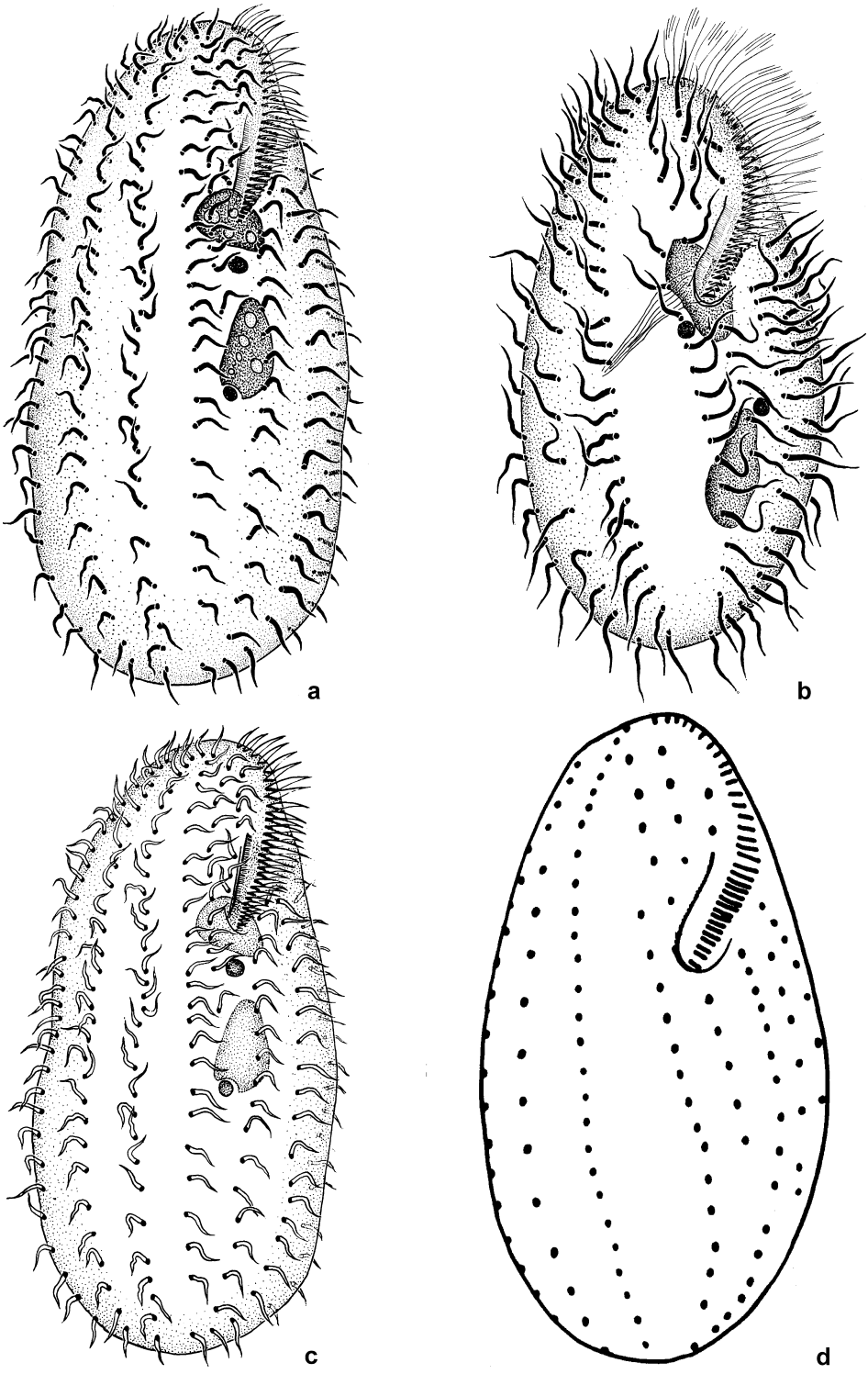
Fig. 63a–d *Kahliella acrobates* (a, b, from Dragesco 1970; c, d, from Dragesco & Dragesco-Kernéis 1986. → Protargol impregnation). Infraciliature of ventral side and nuclear apparatus of "normal" specimen (a, c; 92 µm) and a somewhat deviating specimen (b, d; 88 µm). The cirral pattern is obviously not very exactly illustrated (distances between cirri in parental rows too small) and nothing is known about the dorsal kinety pattern. Thus, the synonymy of *K. acrobates* and *Uroleptopsis multiseta* proposed by Borror (1972) is accepted. Page 354.


a
b
c
d

tion I accept both species until the dorsal kinety pattern of more populations has been checked. However, this implies that *Kahliella acrobates* and *K. simplex* cannot be distinguished without protargol impregnation. Thus, authors which do not check the dorsal infraciliature in detail have to write "*Kahliella acrobates*-group". When no reliable redescription of *K. acrobates* is available until the next detailed revision of the group, then *K. simplex* – for which I fix a neotype in the present review (see there) – should be synonymised with *K. acrobates*, as already proposed by Hemberger (1982).

According to Borror (1972), *Uroleptopsis multiseta* Dragesco, 1970 (= *Kahliella microstoma* in Dragesco & Dragesco-Kernéis 1986) is a junior synonym of *K. acrobates*, a proposal followed by Hemberger (1982, p. 27). I also accept this synonymy because the cirral pattern fits that of *K. acrobates* and nothing is known about the dorsal kinety pattern of *U. multiseta*. The "short" adoral zone is likely an inadequate feature to accept the African population as valid species, although it cannot be excluded that the type population (Fig. 63a) is indeed a distinct species. By contrast, the variety (Fig. 63b) is decidedly a synonym of the *K. acrobates*-group as indicated by the cirral pattern and the "kahliellid" adoral zone.

Hemberger (1982) considered – in contrast to Borror (1972) – *Kahliella multiseta* Dragesco, 1970 as another junior synonym of *K. acrobates*, whereas I classify this species, mainly because of the redescription provided by Dragesco & Dragesco-Kernéis (1986), as junior synonym of *K. simplex*. Dragesco & Dragesco-Kernéis show the dorsal kinety pattern of *K. multiseta* (Fig. 125D in their paper; Fig. 65o in present book), which fits exactly the pattern described by Horváth (1934; Fig. 67f), Berger & Foissner (1987; Fig. 65g), and Eigner (1995; Fig. 70c) for *K. simplex*. Likely par lapsus, Foissner (1987b, p. 230) wrote that Fig. 125D of Dragesco & Dragesco-Kernéis (1986) belongs to *Kahliella microstoma*. However, Dragesco & Dragesco-Kernéis wrote in the legend to this figure that it shows *Kahliella multiseta*, and, in addition, this illustration was provided by Fryd-Versavel, which also provided an original illustration of the cirral pattern of *Kahliella multiseta* (Fig. 124D in Dragesco & Dragesco-Kernéis 1986; Fig. 65n in present book). Borror (1972) considered *Kahliella multiseta* Dragesco, 1970 as valid species.

Grandori & Grandori (1934) used the illustrations by Kahl (1932), but fortunately provided a micrograph and some information about the resting cyst (see below). The illustration by Lundin & West (1963) is not very detailed (Fig. 62l). However, some main features (e.g., "kahliellid" adoral zone, several cirral rows, transverse cirri lacking) are recognisable so that the identification can be accepted. Chardez (1967) made only one illustration, which shows rather strong frontal cirri (Fig. 62m). Tuffrau (1969) made protargol preparations, but he did not study the dorsal ciliature so that it is not known whether or not his identification is correct. He studied the ventral morphogenesis (Fig. 64a–l), which obviously closely resembles that of *K. simplex* (Fig. 70a–o).

Kahliella sp. sensu Fleury & Fryd-Versavel (1982; Fig. 66a, b) and *K. acrobates* sensu Fleury et al. (1985, 1985a) are assigned to *K. simplex* (see there for details).

Morphology: The original description of *K. acrobates* is rather comprehensive. The main problem is the distinct difference in the dorsal kinety pattern of *K. acrobates* and *K. simplex* (dorsomarginal kinety lacking vs. present; see remarks for details). At first the type population is reviewed, followed by supplements from other populations.

Body outline of interphasic specimen as shown in Fig. 62b, that is, left margin straight, right one distinctly convex, both ends broadly rounded; cytoplasm packed with food. Post-divider with slightly convex left margin (Fig. 62a), cytoplasm cloudy; pre-division specimen with parallel margins, bright to translucent and only posterior portion filled with remnants of digested algae (Fig. 62c). Body distinctly flattened dorsoventrally, almost band-shaped; when swimming, anterior third of cell slightly curved dorsad. Two reniform macronuclear nodules slightly left of median; anterior nodule above (not ahead) proximal end of adoral zone, rear nodule distinctly behind mid-body (Fig. 62c). One globular micronucleus attached to left margin of each macronuclear nodule. Contractile vacuole about in mid-body or slightly ahead of it, near left cell margin (Fig. 62a, c); pulsates about every 50–60 s at 21 °C; during diastole with two long collecting canals. Excretion pore slit-like, likely, as is usual, on dorsal side of cell. Sometimes a large, non-pulsating vacuole in frontal area, likely, the parental contractile vacuole, which is present for some time in the rear post-divider. Presence/absence of cortical granules not mentioned. Cytoplasm without peculiarities. Slowly creeping or fast swimming under left or right rotation about main body axis. According to Horváth (1932), creeping is mainly done by the frontal cirri and by the long cirri near the cell margins; when the cell creeps on the dorsal side this is mainly caused by the dorsolaterally and dorsally arranged right marginal row and caudal cirri.

Adoral zone commences at anterior end of cell, terminates at about 42% of body length in specimen shown in Fig. 62b, composed of about 38 membranelles of ordinary structure, that is, membranelles of middle and frontal portion long, proximalmost seven membranelles rather small and very closely arranged. Buccal field narrow, covered by buccal lip. Paroral short, triangular, covering proximal adoral membranelles. Endoral, as is usual, in buccal cavity; longer than paroral; cilia extending into the cytopharynx. Lateral membranellar cilia (= “parorale Cilien” in original description) along whole length of adoral zone. Cytopharynx extends obliquely backwards, without (distinct) supporting fibres. Paroral and endoral move against each other during feeding; however, only the endoral is involved in swallowing.

Cirral pattern as shown in Fig. 62b, d, e, that is, very similar (likely identical) as in *K. simplex* (Fig. 62f, g). Horváth (1932) recognised the cirral pattern very well, but used Stein’s old terminology. In addition, he misinterpreted some features, for example, he assumed that the cirri of frontoventral row II are the anterior portion of the left marginal row. Thus, only relevant data of the original description are provided. At anterior cell end four strong, long cirri, that is, the ordinary three frontal cirri and likely the anteriormost cirrus of row IV; behind these cirri usually a barren area. Eight cirral rows on ventral side; distance between cirri within rows is nar-

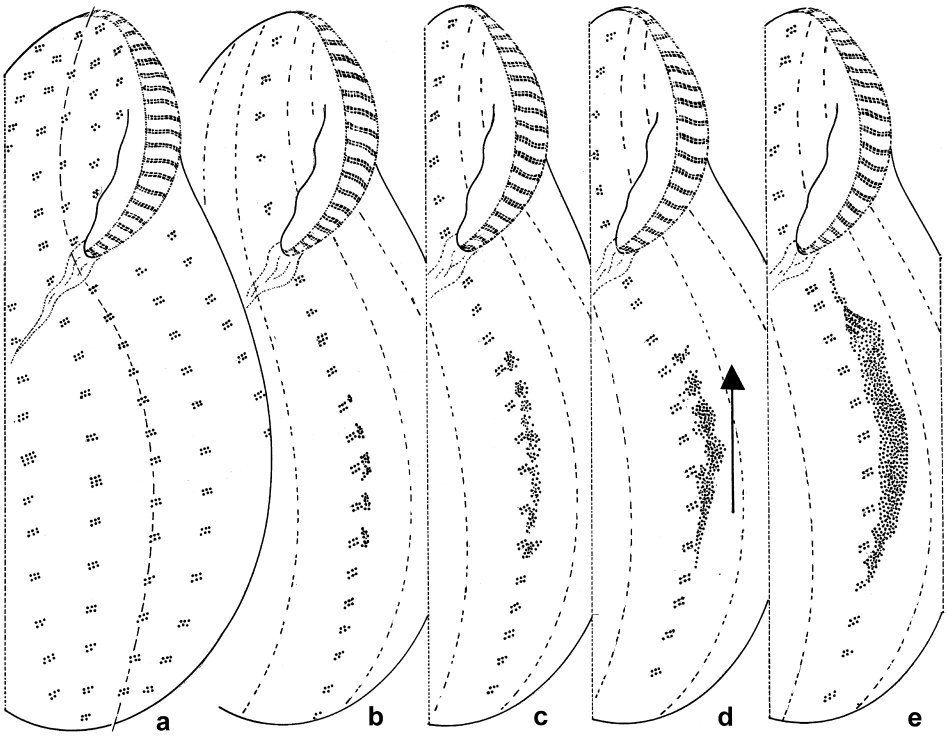


Fig. 64a–e *Kahliella acrobates* (from Tuffrau 1969. Infraciliature of ventral side after protargol impregnation). Interphasic specimen (a) and very early to early dividers. Broken lines connect cirri which originated from the same anlage. Arrow in (d) marks the formation of the oral primordium. For details, see text. Page 354.

rower in central rows than in lateral ones. "Median" cirral row (likely row IV or V) with 24–28 cirri; outermost rows with only 5–7 cirri, which are usually thicker and longer than the cirri in the central cell portion. On right dorsolateral side a long cirral row, which is the ordinary right marginal row. Transverse cirri ("Analcirren" in original description) lacking. For a more detailed description of the cirral pattern, see *K. simplex*.

According to the original description, caudal cirri ("Schwanzcirren" in original description) are lacking because Horváth (1932) did not interpret the cirri of the posterior portion of dorsal kinety 1 as caudal cirri (Fig. 62e). Kinety 1 of specimen illustrated is a combined row, that is, composed of five bristles and eight caudal cirri (Fig. 62e). Between kinety 1 and right marginal row four bristle rows roughly of body length. According to Fig. 62e, a posteriorly distinctly shortened dorsomarginal kinety is lacking (see remarks for detailed discussion of that problem). Bristles short (likely 3–5 µm), but stronger and more rigid than cilia of cirri. In rows 2 and 5 often some bristles lacking.

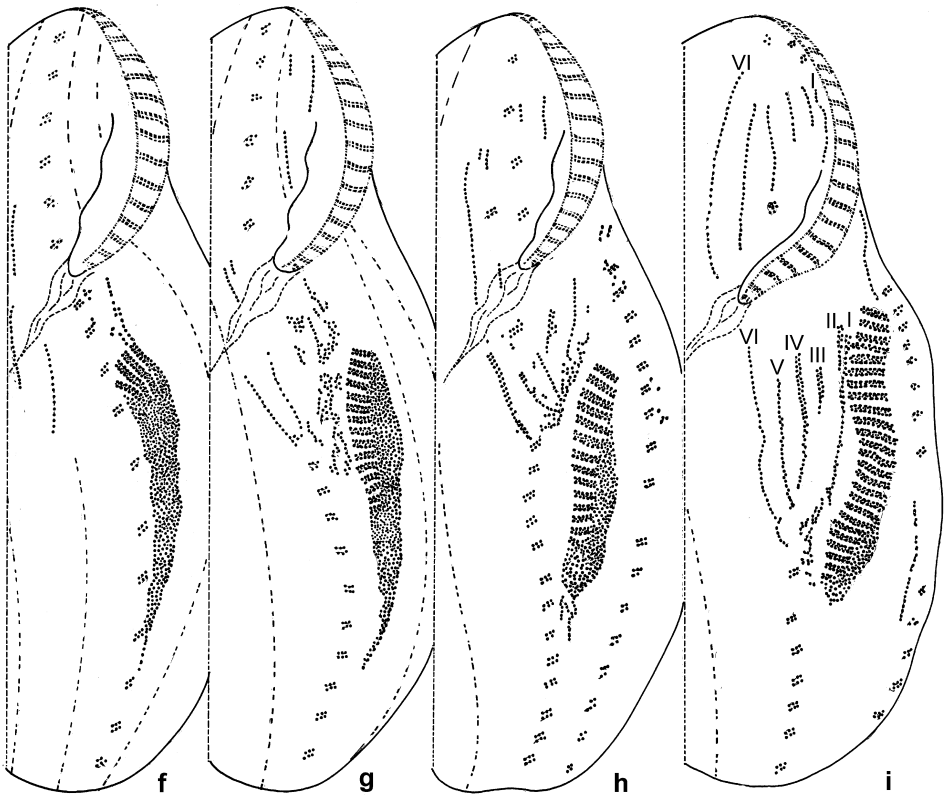


Fig. 64f–i *Kahliella acrobates* (from Tuffrau 1969. Infraciliature of ventral side after protargol impregnation). Middle and late dividers showing formation of adoral membranelles and frontoventral anlagen in proter and opisthe. For details see text. I–VI = frontal-ventral cirri anlagen. Page 354.

Population studied by Kahl (1932; Fig. 62j, k; only deviating and supplemental features mentioned): body length 100–200 µm, length:width ratio of specimen shown in Fig. 62j about 2.8:1. Body slightly to moderately flattened dorsoventrally, soft and flexible; without ridges. Usually two macronuclear nodules; however, in well flourishing cultures number of nodules rather variable. Posterior cell portion usually with a dark (refractive?) agglomeration of excretion granules. Usually lively rotating. Anterior and middle portion of adoral zone extends along cell margin, proximal portion bends obliquely to near cell midline. Eight cirral rows arranged as shown in Fig. 62j, k. Three dorsal kineties of body length (Fig. 62k) against four in type population (Fig. 62e) and two in *K. simplex* (Fig. 65g, 67f); cilia short and fine.

Specimens studied by Tuffrau (1969) around 170 µm long; outline roughly pyriform; 7–10 uniform cirral rows.

Dragesco (1970) described two populations of the synonym *Uroleptopsis multiseta*, but nothing is known about the important dorsal ciliature. Type population (Fig. 63a, c) with rather short (about 30% of body length) adoral zone composed of

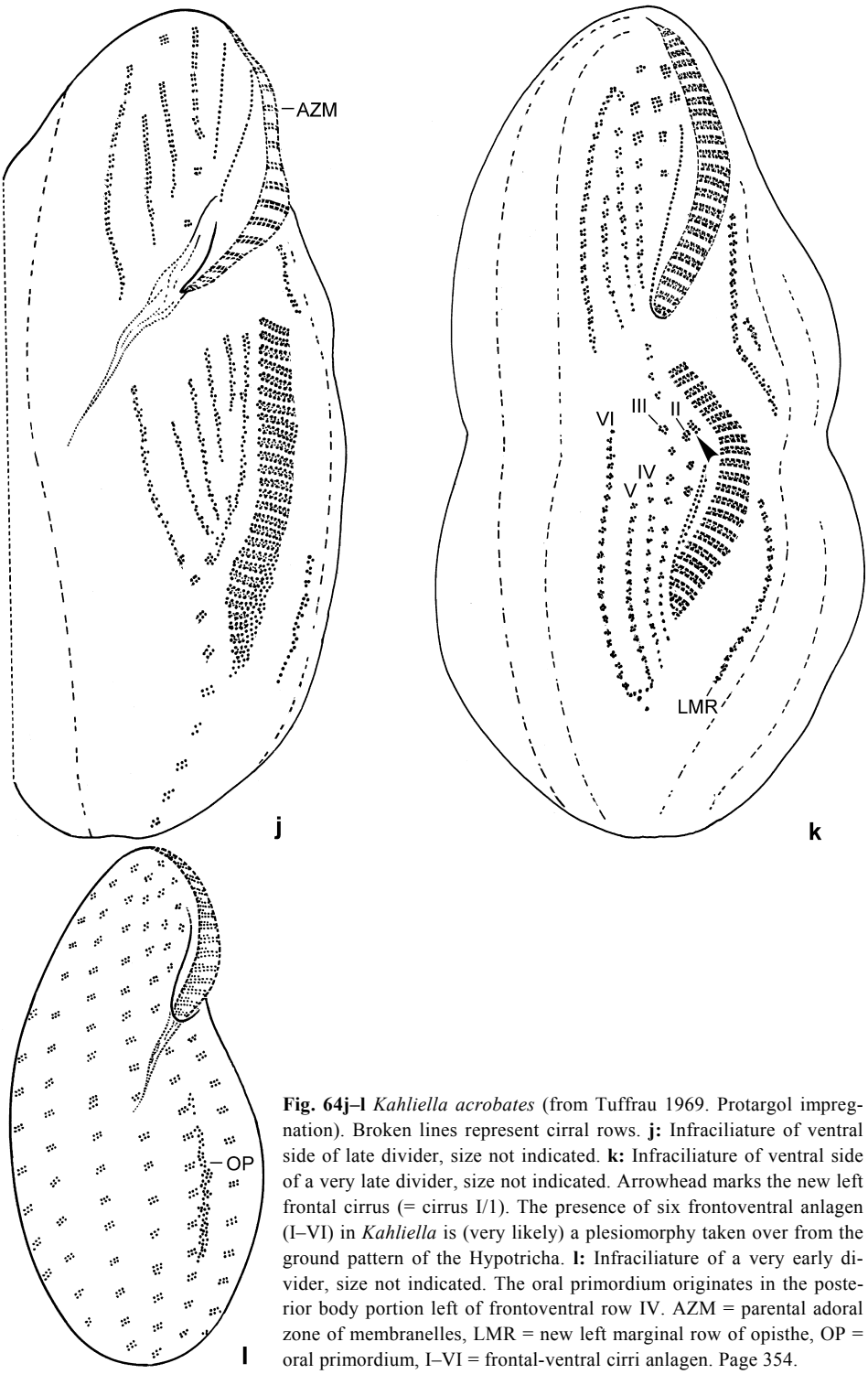


Fig. 64j–l *Kahliella acrobates* (from Tuffrau 1969. Protargol impregnation). Broken lines represent cirral rows. **j:** Infraciliature of ventral side of late divider, size not indicated. **k:** Infraciliature of ventral side of a very late divider, size not indicated. Arrowhead marks the new left frontal cirrus (= cirrus I/1). The presence of six frontoventral anlagen (I–VI) in *Kahliella* is (very likely) a plesiomorphy taken over from the ground pattern of the Hypotricha. **l:** Infraciliature of a very early divider, size not indicated. The oral primordium originates in the posterior body portion left of frontoventral row IV. AZM = parental adoral zone of membranelles, LMR = new left marginal row of opisthe, OP = oral primordium, I–VI = frontal-ventral cirri anlagen. Page 354.

about 28–30 membranelles. Two macronuclear nodules, each 11–15 µm long, two micronuclei each 2–3 µm across. Second population about 85–95 µm long (Fig. 63b, d); macronuclear nodules 15–30 µm long, micronuclei about 3 µm across; contractile vacuole near left cell margin about in mid-body; adoral zone about 38% of body length. Cirral pattern of both populations rather variable.

According to Fauré-Fremiet (1957), the cytoplasm of *K. acrobates* contains anisotropic, mineral concretions (for review, see Dutta 1974, p. 313). Olins & Olins (1994, p. 150) estimated, from the micrographs published by Fleury et al. (1985), that the chromatin fibres of the forward zone of the replication band are about 55 nm thick.

Cell division: Morphogenesis of the ventral side was studied by Tuffrau (1969, Fig. 64a–l).[1] It commences with the formation of an oral primordium originating from (close to?) the posterior cirri of frontoventral row IV (Tuffrau 1970; Fig. 64b). The further process is obviously very similar to that of *Kahliella simplex* which was studied in detail by Eigner (1995). Six frontoventral cirral anlagen are formed, a feature taken over from the ground pattern of the Hypotricha (Berger 2008). Unfortunately, the dorsal kinety formation (presence/absence of a dorsomarginal row) is not described. Macronuclear nodules fuse, as is usual, to a single mass during cell division (Horváth 1932).

Conjugation: Horváth (1932) could never observe or artificially induce conjugation.

Cyst: Fauré-Fremiet (1957, p. 106) found an agglomeration of calcareous microcrystals outside the cyst wall. The same feature is recognisable in the photomicrograph provided by Grandori & Grandori (1934, Fig. XXXIV C). Unfortunately, the quality of the micrograph is not very good so that it cannot be reproduced here. Later, this feature was described for *K. simplex* (Foissner I. & Foissner W. 1987; Fig. 69a).

Occurrence and ecology: Very likely, *Kahliella acrobates* prefers terrestrial habitats (Foissner 1998, p. 204). Although Horváth (1932, p. 425) studied a soil sample, he wrote in the diagnosis (see corresponding footnote above) that *K. acrobates* lives in stagnant waters, which is somewhat misleading.

Unfortunately, the type locality of *K. acrobates* is not clearly described, which is a reason to fix a neotype (ICZN 1999, Article 75.3.1). According to Horváth (1932), the culture containing the type population was established in "April of the last year" in that soil from the garden of the institute was put into a vessel with gelatine on the bottom and poured with tap water. The question is whether the soil sample was from the University of Szeged (Hungary), where Horváth usually lived and worked, or from the "Institut für Schiffs- und Tropenkrankheiten zu Hamburg" in the city of Hamburg (Germany), where Horváth was for research purposes and obviously drafted the original description (Horváth 1932). Horváth (1936, p. 482) wrote that he has discovered *Kahlia* in 1931 and studied it in the above mentioned institute in Hamburg. In addition, he reported that he has found *K. simplex* in the flower-garden

[1] Likely the abstract by Tuffrau (1968) also refers to this species/population.

of the University of Szeged (at Szukováthy-Place) were *K. acrobates* also occurs. I suppose that Horváth (1932) collected the soil sample containing *K. acrobates* from the Szeged area and took the culture to Hamburg where he studied it in Kahl's and Reichenow's custody. If my interpretation of the somewhat confusing locality-data is correct, then the type locality of *K. acrobates* is, like that of *K. simplex*, in Szeged (ICZN 1999, Article 76.1.1). This would be, however, a further hint that *K. acrobates* and *K. simplex* are the same. The abundance of *K. acrobates* in Horváth's (1932) culture was high, few specimens of *Colpoda fastigata* Kahl (a junior synonym of *C. maupasi* Enriques; for review, see Foissner 1993) and *Chilodon* sp. were present, and the pH of the culture water was 8.7.

Kahl (1932) found *K. acrobates* in great number in an infusion of garden soil established by Eduard Reichenow; unfortunately, the sampling site of this population is not mentioned. Type locality of the synonym *Uroleptopsis multiseta* (= *Kahliella microstoma*) is Yaounde, Cameroon (Dragesco 1970, habitat not specified; see also Dragesco 1980, p. 181 and Dragesco & Dragesco-Kernéis 1986).

Records substantiated by morphological data: soil in Belgium (Chardez 1967; 1987, p. 13); ditch(?) from near a farm in the region de Limours (Essonne), France (Tuffrau 1969); soil of heathland (*Callunetum*) in Italy (Grandori & Grandori 1934); soil in USSR (Nikoljuk & Geltzer 1972, p. 129; illustrations from Kahl 1932); limnetic habitats in Marquette, Upper Peninsula of Michigan, USA (Lundin & West 1963; West 1953, p. 282; West & Lundin 1963, p. 106).

Records not substantiated by morphological data: ditch near a farm in the vicinity of Orsay, France (Fauré-Fremiet 1961, p. 311); with moderate abundance in a chernozem soil in the centre of the Great Hungarian Plain (Szabó 2000, p. 14); soil of a macchia near Rome, Italy (Luzzatti 1938, p. 100); in an experiment on the effect of the herbicide Monuron in the drainage system of Turkmen (Gel'cer & Geptner 1976, p. 177); Donghu Lake, Wachang, China (Shen & Gu 1965, Table 4); fresh water bodies on Mount Desert Island (McCashland 1956, p. 38); Savannah River (USA) in the Coastal Plain region at 20–23°C, >5.0–7.0 mg l^{-1} O_2, 0.05 to <1.0 mg l^{-1} NH_3-N (Patrick et al. 1967, p. 321); limnetic habitats in southeastern Louisiana, USA (Bamforth 1963, p. 133); Waipahihi Stream in the Taupo Thermal Region in New Zealand at 33.5 °C during June 1966 (Winterbourn & Brown 1967, p. 46).

Chardez (1988, p. 9) mentioned *Kahliella acrobates* and its synonym *K. microstoma* in a paper about criminology.

Kahliella acrobates feeds on bacteria, algae, and ciliates like *Colpoda* (Horváth 1932); according to Kahl (1932) it ingests small globular algae and likely *Colpoda fastigata*. Tuffrau (1969) cultured *K. acrobates* in the presence of *Chilomonas* and *Colpidium*. According to Szabó (2000) it feeds on bacteria and diatoms. Further, it multiplies on *Polytoma uvella* (good growth) and *P. caudatum* (poor growth) in meat peptone, but not on two strains of *Polytomella agilis* (Provasoli 1935; Kidder 1951, p. 142); no growth occurred when living flagellates were replaced by flagellates heated for 9 min at 44°C, macerated fresh liver, liver extract plus dead yeast plus fresh rabbit kidney, or heat killed bacteria. Provasoli (1935) concluded from these

data that *P. uvella* contained a very heat-labile compound essential for the growth of *K. acrobates*. This compound or complex was not present in *P. agilis* and was present in suboptimal amounts in *Polytoma caudatum* (for review, see van Wagtendonk 1955, p. 60). According to Provasoli (1935) and Provasoli et al. (1958, p. 27), *Kahliella acrobates* can be cultured in a lettuce or Cerophyl medium.

Kahliella simplex (Horváth, 1934) comb. nov.

(Fig. 4a, b, 65a–o, 66a, b, 67a–z, 68a–e, 69a–d, 70a–o, 71a–g, Table 22)

1934 ***Kahlia simplex* nov. sp.** – Horváth, Acta Litt. Scient. R. Univ. hung. Francisco-Josephina, Acta biologica, 3: 60, 1 táblával ("Tafel II") with Figures 1–12 (Fig. 67a–h; original description in Hungarian; no formal diagnosis provided; likely no type material available, see nomenclature of *K. acrobates*).

1936 ***Kahlia simplex*** – Horváth, Arch. Protistenk., 86: 482, Fig. 1–11 (Fig. 67i–r; physiology and morphogenesis).

1954 ***Kahlia simplex*** – Stout, Trans. R. Soc. N. Z., 82: 203, Fig. 12 (Fig. 67s; illustrated record from a meat digestion plant).

1960 ***Kahlia simplex* Horváth** – Ördögh, Acta biol. hung., 10: 127, Abb. 1–7 (Fig. 67t–z; nuclear division).

1970 ***Kahliella multiseta* n. sp.** – Dragesco, Annls Fac. Sci. Univ. féd. Cameroun, Numéro hors-série: 105, Fig. 77A, B, 78 (Fig. 65h, i, 68a–e; original description of new synonym; no formal diagnosis provided; likely no type material deposited [Aescht 2008, p. 194]).

1972 ***Kahliella simplex* (Horváth, 1934) Corliss, 1960** – Borror, J. Protozool., 19: 9 (revision of hypotrichs; see nomenclature).

1982 ***Kahliella* sp.** – Fleury & Fryd-Versavel, Protistologica, 18: 135, Fig. 1–10, Tableau 1 (Fig. 66a, b, 70l–o, 71a–g; description of morphology, cell division, conjugation, and reorganisation).

1985 ***Kahliella acrobates*** – Fleury, Iftode, Deroux & Fryd-Versavel, Protistologica, 21: 508, Fig. 3, 8–24 (electron microscopic study; misidentification).

1986 ***Kahliella multiseta* Dragesco, 1970** – Dragesco & Dragesco-Kernéis, Faune Tropicale 26: 427, Planche 124 A–E, Planche 125 D (Fig. 65j–o; redescription of synonym).

1987 ***Kahliella simplex* (Horváth, 1934) Corliss, 1960** – Berger & Foissner, Zool. Jb. Syst., 114: 201, Fig. 18–24, Table 4 (Fig. 65a–g; detailed redescription; 1 voucher slide is deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; see neotypification).

1987 ***Kahliella simplex*** – Foissner & Foissner, Zool. Anz., 218: 66, Fig. 1–9 (Fig. 69a–d; fine structure of resting cyst).

1988 ***Kahliella simplex*** – Berger & Foissner, Arch. Protistenk., 136: 67, Fig. 2 (Fig. 65f; comparison with *Kahliella franzi*, now *Neowallackia franzi*).

1995 ***Kahliella simplex* (Horváth, 1934) Corliss, 1960** – Eigner, Europ. J. Protistol., 31: 353, Fig. 29–38, 47, Table 3 (Fig. 70a–k; detailed description of cell division).

2001 ***Kahliella simplex* (Horváth, 1934) Corliss, 1960** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 40 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: Unfortunately, the description of *K. simplex* is in Hungarian without German or English summary. Thus, I do not know whether or not Horváth provided a derivation of the species-group name *simplex* (Latin; simple, natural; Hentschel & Wagner 1996); possibly it refers to the number of cirri/cirral rows and dorsal kineties which is somewhat lower ("more simple") than in *K. acrobates*. The species-group name *multiseta* is a composite of the Latin quantifier *mult-* (many), the the-

Table 22 Morphometric data on *Kahliella acrobates* (ac1, from Horváth 1932; ac2, synonym *Uroleptopsis multiseta* [Fig. 63a] from Dragesco 1970) and *Kahliella simplex* (si1, from Berger & Foissner 1987; si2, from Eigner 1995; si3, Cotonou population from Dragesco & Dragesco-Kernéis 1986)

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Body, length	ac2	–	–	–	–	–	75.0	95.0	?
	si1	114.6	108.0	13.5	3.1	11.8	92.0	140.0	19
	si2	140.1	142.0	13.7	–	9.8	100.0	162.0	15
Body, width	si1	44.2	43.0	4.4	1.0	10.1	36.0	52.0	19
	si2	50.0	50.0	6.3	–	12.6	36.0	60.0	15
Adoral zone of membranelles, length	si1	41.6	42.0	4.1	0.9	9.9	36.0	53.0	19
	si2	47.1	46.0	2.0	–	4.2	44.0	50.0	15
Anterior body end to anterior end of frontoventral row V, distance	si1	30.4	29.0	4.5	1.0	14.7	22.0	39.0	19
Anterior macronuclear nodule, length	ac2 [h]	–	–	–	–	–	11.0	15.0	?
	si2	27.1	26.0	4.3	–	15.7	20.0	34.0	15
Anterior macronuclear nodule, width	si2	8.5	8.0	1.1	–	13.2	7.0	10.0	15
Posterior macronuclear nodule, length	si1	18.3	18.0	2.3	0.5	12.5	15.0	22.0	19
	si2	30.0	32.0	4.3	–	14.2	24.0	40.0	15
Posterior macronuclear nodule, width	si1	8.1	8.0	1.6	0.4	19.2	7.0	14.0	19
	si2	8.2	8.0	1.2	–	14.7	7.0	10.0	15
Macronuclear nodules, distance in between	si1	16.6	17.0	4.1	0.9	24.4	7.0	22.0	16
Micronucleus, diameter	si1	3.4	3.5	0.3	0.1	9.5	3.0	4.0	19
Adoral membranelles, number	ac1	38.0	–	–	–	–	–	–	?
	si1	36.8	36.0	2.7	0.6	7.4	33.0	44.0	19
	si2	41.6	42.0	2.6	–	6.1	36.0	46.0	15
	si3 [g]	–	–	–	–	–	34.0	40.0	12
Frontal cirri, number	si1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Enlarged cirri in frontal field, number [e]	si2	13.0	13.0	–	–	–	12.0	14.0	15
Buccal cirri, number [f]	si2	1.0	1.0	–	–	–	0.0	2.0	15
Frontoventral row I, number of cirri	si2	1.0	1.0	–	–	–	1.0	1.0	15
Frontoventral row II, number of cirri [b, c]	si1	2.2	2.0	0.4	0.1	18.9	2.0	3.0	19
	si2	2.9	3.0	0.5	–	17.8	2.0	4.0	15
Frontoventral row III, number of cirri [b, c]	si1	4.1	4.0	0.4	0.1	9.9	3.0	5.0	19
	si2	4.7	5.0	0.6	–	9.7	4.0	5.0	15
Frontoventral row IV, number of cirri [b]	si1	14.7	15.0	2.1	0.5	14.5	11.0	18.0	19
	si2	13.1	15.0	4.3	–	32.7	4.0	20.0	15
Frontoventral row V, number of cirri [b]	si1	17.2	17.0	2.0	0.5	11.9	13.0	21.0	19
	si2	14.6	17.0	6.9	–	47.2	2.0	25.0	15
Frontoventral row Va, number of cirri [b]	si2	17.7	19.0	7.0	–	39.8	6.0	27.0	10
Frontoventral row VI, number of cirri [b]	si1	31.4	32.0	3.8	0.9	12.2	24.0	39.0	19
	si2	36.9	37.0	4.2	–	11.5	27.0	43.0	15
Frontoventral row VI (+1), number of cirri [b]	si1	15.6	15.0	4.8	1.1	30.8	10.0	30.0	19
	si2	18.6	20.0	2.7	–	14.3	14.0	24.0	15
Frontoventral row VI (+2), number of cirri [b]	si1	7.6	7.0	2.8	0.6	36.9	3.0	14.0	19
	si2	8.1	8.0	1.4	–	17.7	6.0	10.0	15
Frontoventral row VI (+3), number of cirri [b]	si1	4.8	5.0	2.1	0.5	42.6	2.0	8.0	19
	si2	4.5	5.0	–	–	–	3.0	6.0	15
Right marginal row, number of cirri [b]	si1	24.9	26.0	2.7	0.6	10.9	19.0	30.0	19
	si2	28.3	30.0	2.7	–	9.5	21.0	31.0	15
Left marginal row, number of cirri [b]	si1	20.6	21.0	2.6	0.6	12.8	16.0	26.0	19
	si2	24.4	25.0	2.9	–	11.8	18.0	29.0	15

Table 22 Continued

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Left marginal row (+1), number of cirri [b]	si1	9.1	9.0	3.5	0.8	38.5	4.0	18.0	19
	si2	9.7	10.0	1.7	–	17.6	7.0	13.0	15
Left marginal row (+2), number of cirri [b]	si1	5.5	6.0	2.6	0.6	48.0	2.0	13.0	19
	si2	5.9	6.0	0.9	–	15.4	5.0	8.0	15
Left marginal row (+3), number of cirri	si2	4.0	4.0	–	–	–	4.0	6.0	15
Macronuclear nodules, number	si1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	si2	2.0	2.0	–	–	–	2.0	4.0	15
Micronuclei, number	si1	1.5	1.0	0.5	0.1	34.8	1.0	2.0	19
	si2	2.0	2.0	–	–	–	2.0	4.0	15
Dorsal kineties, number [d]	si1	4.0	4.0	0.0	0.0	0.0	4.0	4.0	19
	si2	3.0	0.0	–	–	–	3.0	3.0	15
Dorsal kinety 1, number of bristles	si1	8.2	8.0	1.4	0.3	16.5	6.0	11.0	19
Caudal cirri, number [b]	si1	10.9	11.0	1.4	0.3	12.3	8.0	13.0	19
	si2	12.1	8.0	2.4	–	19.9	6.0	16.0	15

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known), SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] In *K. simplex* the cirral rows have the following designation in Berger & Foissner (1987) / Eigner (1995): caudal cirri = cirral row 1 (dorsal bristles not included) / IL2 (number of cirri); frontoventral II = frontal row I / I2; frontoventral row III = frontal row II / I3; frontoventral row IV = cirral row 5 / I4; frontoventral row V = cirral row 6 / I5; frontoventral row Va = – / I6; frontoventral row VI = cirral row 7 / I7; frontoventral row VI (+1) = cirral row 8 / P1; frontoventral row VI (+2) = cirral row 9 / P2; frontoventral row VI (+3) = cirral row 10 / P3; left marginal row = cirral row 4 / IL1; left marginal row (+1) = cirral row 3 / PL1; left marginal row (+2) = cirral row 2 / PL2; left marginal row (+3) = – / PL3; right marginal row = cirral row 11 / I8.

[c] Frontal cirri included (si1).

[d] Berger & Foissner (1987) did not include the row with the caudal cirri (= dorsal kinety 1 in present paper), thus, they counted only three kineties. Eigner (1995) also did not count the row marked with "1" in Fig. 65g as dorsal kinety; thus, he also counted only three dorsal kineties.

[e] Eigner (1995) did not clearly indicate which cirri are included.

[f] No detailed explanation given; likely all cirri of anlage II which are close to the undulating membranes.

[g] Dragesco & Dragesco-Kernéis (1986) mention 33 as mean; this is likely incorrect because the extremes are 34 and 40.

[h] Nodule (anterior or posterior) not indicated.

matic vowel ·*i*-, and the Latin noun *seta* (hair, cirrus in present case) and obviously alludes to the high number of cirri.

Although Corliss (1960) did not mention *Kahlia simplex* or *Kahliella simplex*, he is generally accepted as combining author, for example, by Borror (1972), Berger & Foissner (1987), Eigner (1995), Foissner (1998, p. 204), and Berger (2001). However, I found no article in the ICZN (1999) or previous editions which decides that all species-group names are automatically combined when a substitute genus-group

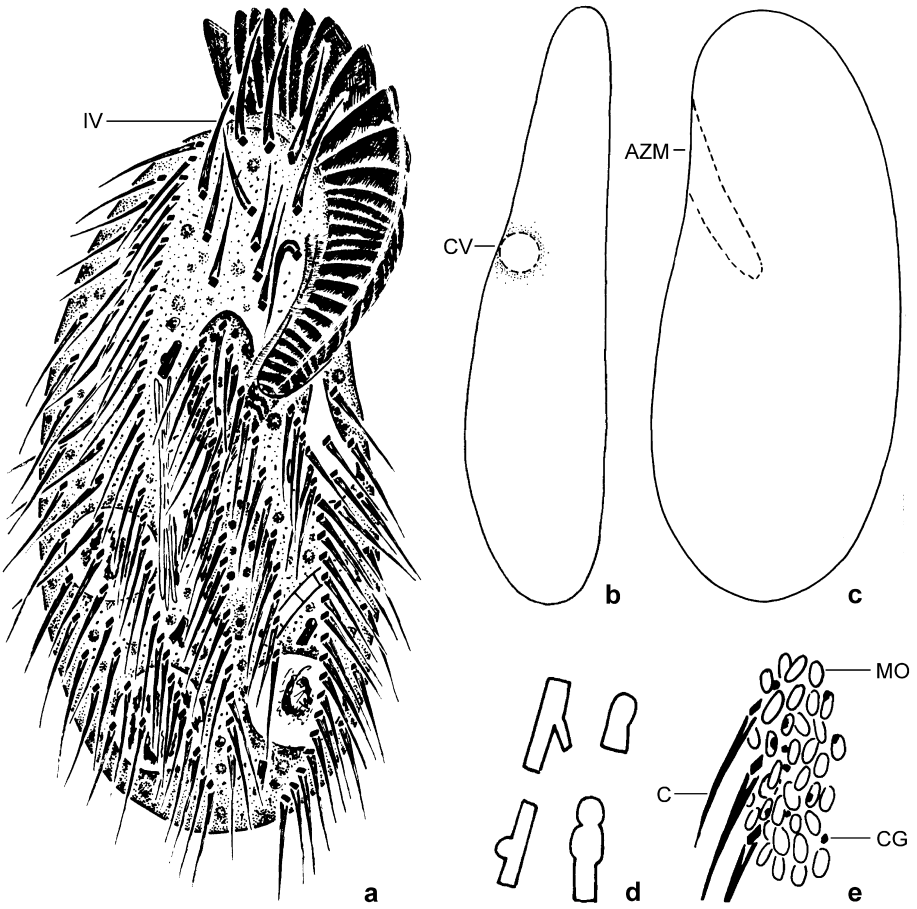


Fig. 65a–e *Kahliella simplex* (from Berger & Foissner 1987. From life). **a:** Ventral view of a representative specimen, 122 µm. **b:** Right lateral view showing contractile vacuole. **c:** Outline in dorsal view. **d:** Cytoplasmic crystals, 2–5 µm. **e:** Part of cortex showing cirri, colourless cortical granules (<1 µm across), and ellipsoidal structures (likely mitochondria; 1–3 µm) close underneath. AZM = adoral zone of membranelles, C = cirrus, CG = cortical granule, CV = contractile vacuole, MO = mitochondrium, IV = frontoventral row IV. Page 367.

name is introduced. Thus, Corliss (1960) should not be considered as combining author for *Kahliella simplex*, simply because one cannot make an entry in the list of synonyms. Since *Kahlia simplex* Horváth, 1934 was never formally transferred to *Kahliella* Corliss, 1960, this nomenclatural act has to be made up here (see heading on p. 367).

Neotypification: According to Berger & Foissner (1987, p. 195), one slide of the Austrian population has been deposited in the Upper Austrian Museum (= Oberösterreichisches Landesmuseum) in Linz (LI). Finally, however, we have deposited four slides (accession numbers 1986/57–60), which we designated as neotypes

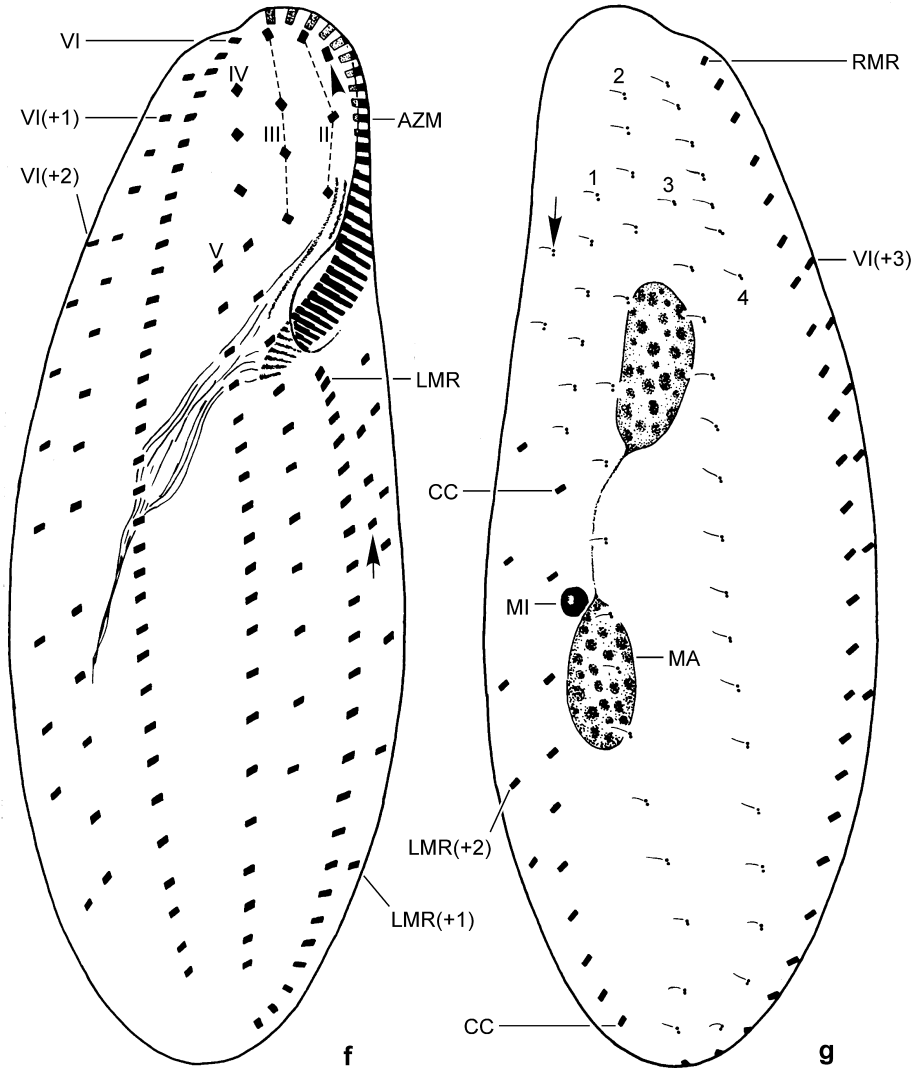


Fig. 65f, g *Kahliella simplex* (from Berger & Foissner 1987. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of neotype specimen, 120 µm. Arrowhead in (f) marks left frontal cirrus (= cirrus I/1), arrow in (f) denotes a very short additional parental left marginal row not considered in the morphometry. Arrow in (g) marks two (parental?) dorsal bristles. AZM = adoral zone of membranelles, CC = caudal cirri (= rear portion of dorsal kinety 1), LMR = left marginal row, LMR(+1), LMR(+2) = left marginal rows of previous generations, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row, I–VI = frontoventral cirri rows, VI(+1), VI(+2), VI(+3) = frontoventral row VI of previous generations, 1–4 = dorsal kineties (4 is a dorsomarginal kinety). Page 367.

(Aescht 2003, p. 396; 2008, p. 178). However, since our paper (Berger & Foissner 1987) does not contain any hint on such a nomenclatural act, this "neotypification"

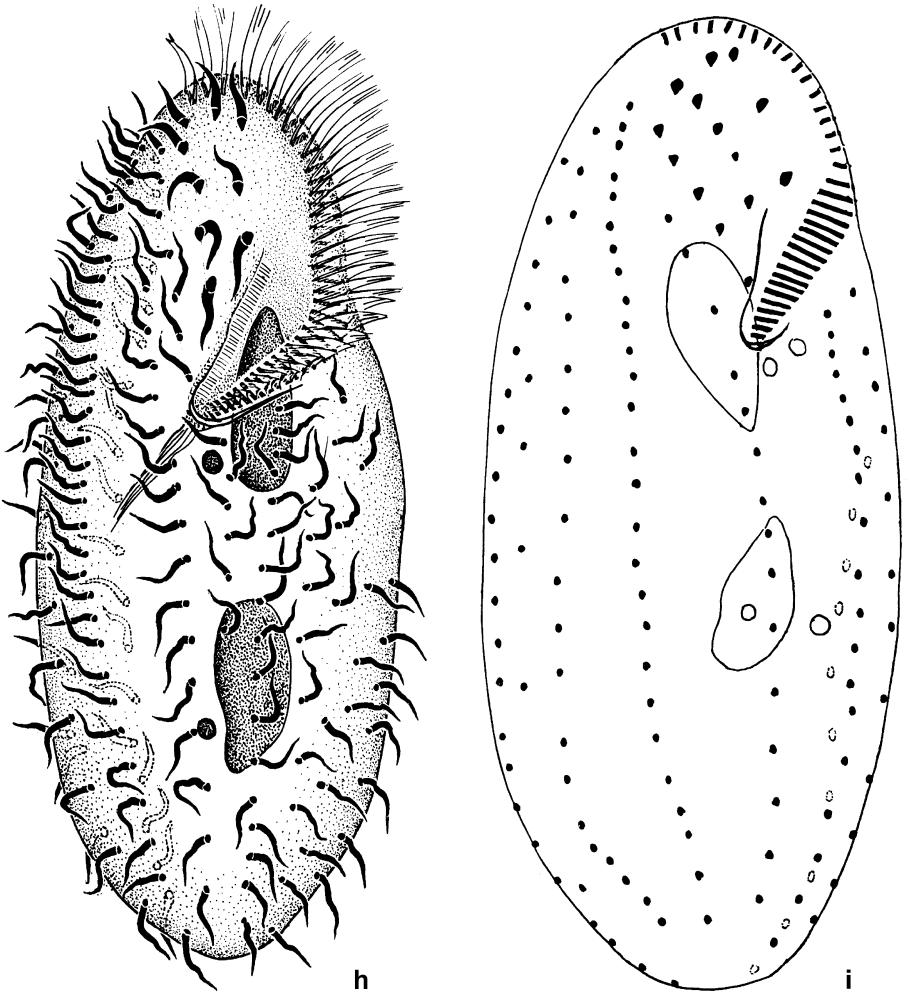


Fig. 65h, i *Kahliella simplex* (from Dragesco 1970. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus, 91 µm. I suppose that the cirral pattern is not very exactly illustrated. Page 367.

is invalid; it comes under Article 75.2 of the ICZN (1999). Actually these four slides are voucher slides.

Synonymy of *K. acrobates* and *K. simplex* cannot be excluded (see remarks at type species). Unfortunately, type material of both species is very likely not available so that neotypifications are needed to define both taxa objectively and, subsequently, to solve the somewhat tricky situation seriously. As a first step, the Austrian population described by Berger & Foissner (1987) is fixed as neotype of *Kahliella simplex* (note that the "neotypification" discussed in the previous para-

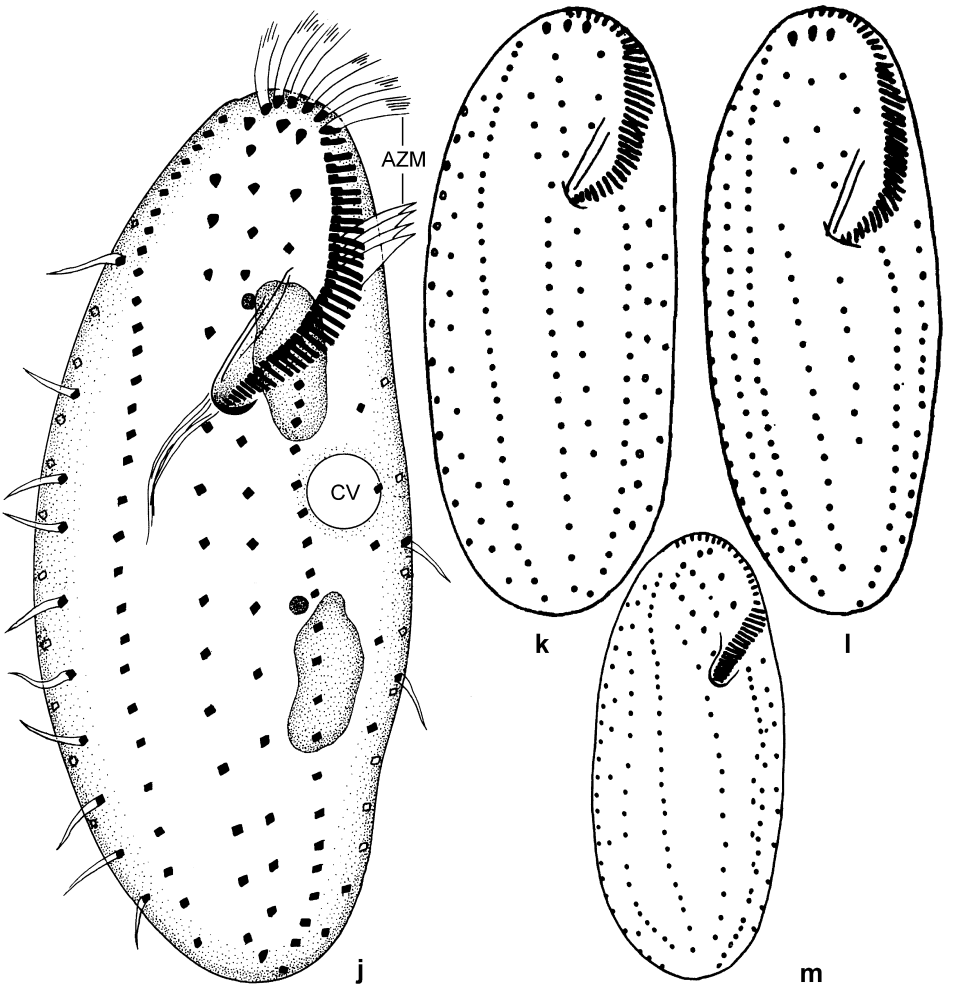


Fig. 65j–m *Kahliella simplex* (j–l, from Dragesco & Dragesco-Kernéis 1986; m, after Dragesco 1970 from Dragesco & Dragesco-Kernéis 1986. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus, j = 90 µm, k, l = size not indicated, m = 91 µm. AZM = adoral zone of membranelles, CV = contractile vacuole. Page 367.

graph is invalid). To make the neotypification valid, the following particulars have to be published (ICZN 1999, Article 75.3):

(i) It cannot be excluded that *K. acrobates* (type species) and *K. simplex* are synonymous (see remarks at *K. acrobates* for detailed discussion).

(ii) *Kahliella acrobates* and *K. simplex* differ only in the dorsal kinety pattern. The pattern of *K. simplex* reported in the original description has been confirmed in several redescriptions, including that by Berger & Foissner (1987; cp. Fig. 65g, 67f).

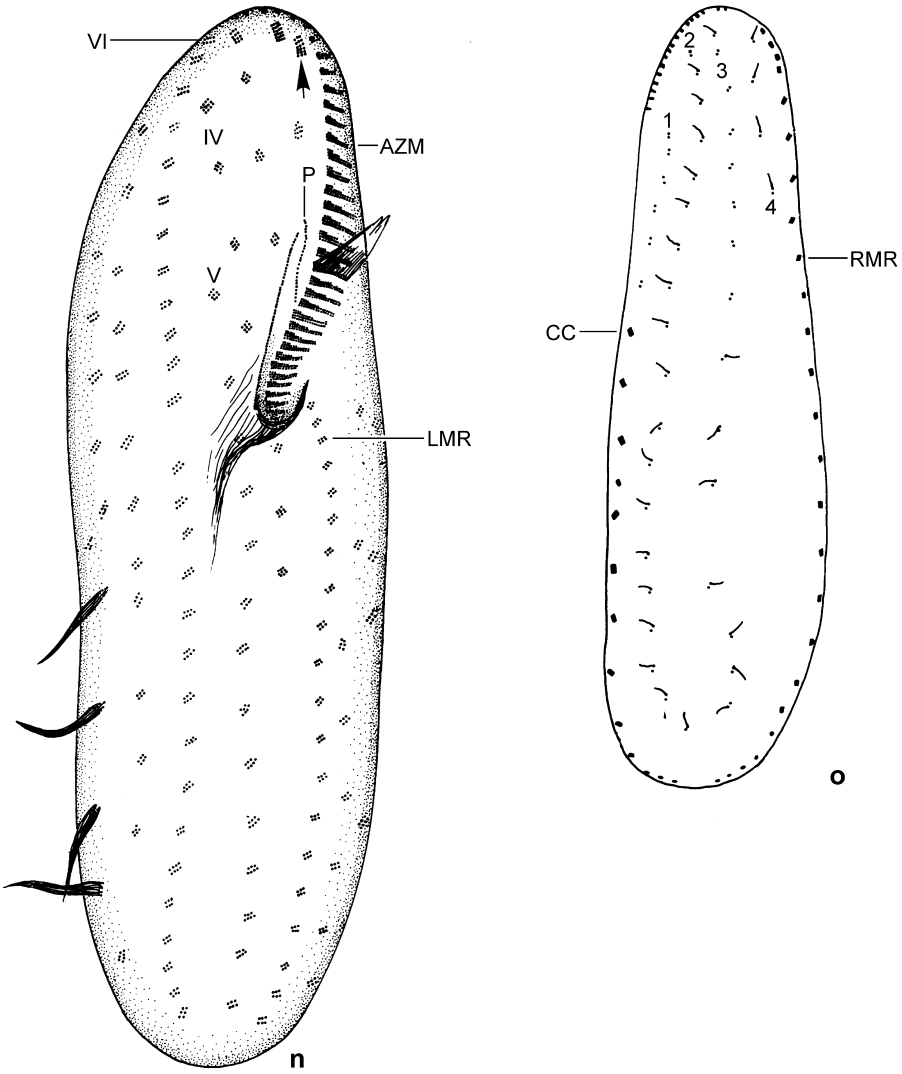


Fig. 65n, o *Kahliella simplex* (originals provided by Fryd-Versavel from Dragesco & Dragesco-Kernéis 1986. Protargol impregnation). Infraciliature of ventral and dorsal side of different specimens, sizes not indicated. Arrow in (n) marks left frontal cirrus (cirrus I/1). Note that the infraciliature agrees very well with that of the neotype population (Fig. 65f, g). AZM = adoral zone of membranelles, CC = anteriormost caudal cirrus, LMR = left marginal row, P = paroral, RMR = right marginal row, IV–VI = frontoventral rows, 1–4 = dorsal kineties (kinety 4 is the dorsomarginal row). Page 367.

The pattern originally described for *K. acrobates* is not yet confirmed; thus it cannot be excluded that Fig. 62e is a misobservation.

(iii) The specimen illustrated by Berger & Foissner (1987, Fig. 23, 24; Fig. 65f, g in present book) is designated as neotype specimen. It is contained in one (originally

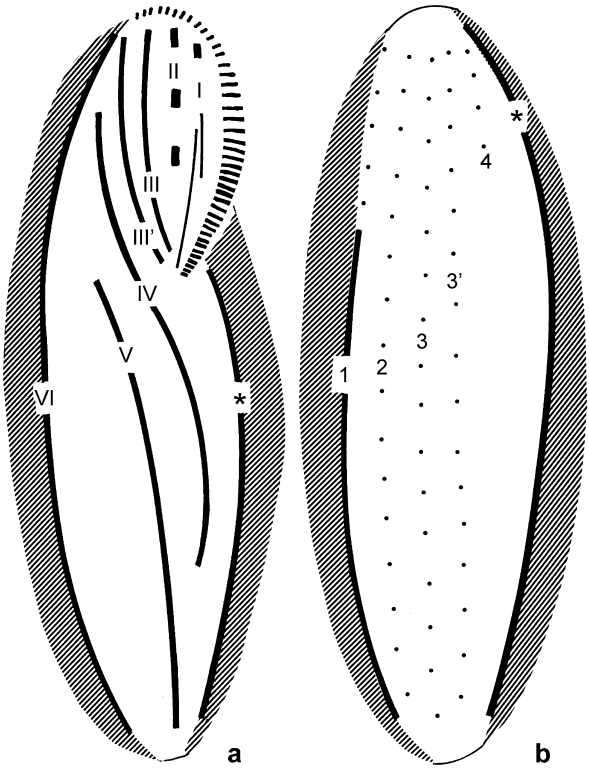


Fig. 66a, b *Kahliella simplex* (from Fleury & Fryd-Versavel 1982). Schematic illustration of ventral and dorsal infraciliature. In the hatched areas the parental rows are located (cp. Fig. 65f, g). Asterisks mark left (a), respectively, right (b) marginal row. I–VI = frontoventral rows (row III' is lacking in about 50% of specimens), 1–4 = dorsal kineties (kinety 3' is present in 1 of 20 specimens). Page 367.

designated as slide P52) of the four neotype slides deposited in the Museum in Linz (see [vii] for details).

(iv) Horváth (1934) stained the cirri and dorsal bristles after mordanting with phosphor-wolfram-acid. According to Horváth (1937, p. 55), such a stain "is rather stable", indicating that the permanent slides are usable for several years, but not for 70 years or more, that is, until now. In addition, I did not find a paper containing a hint about the whereabouts of the slides made by János Horváth who worked at the University of Szeged (Hungary). However, I did not contact the University about that problem. Anyhow, I strongly suppose that the type material of *K. simplex* is no longer available. Of course the present neotypification is invalid when type material – showing the dorsal kinety pattern, that is, the relevant feature – is found still to exist (ICZN 1999, Article 75.8).

(v) The Austrian population of *K. simplex* described by Berger & Foissner (1987; Fig. 65a–g) matches perfectly the original description (Fig. 67a–h). Thus, the identification by Berger & Foissner (1987) is beyond reasonable doubts. In addition, it is the sole population described both from life and after protargol preparations.

(vi) The original type locality is the soil of the flower-garden of the University of Szeged, Hungary. The neotype population was isolated from the upper soil layer of a

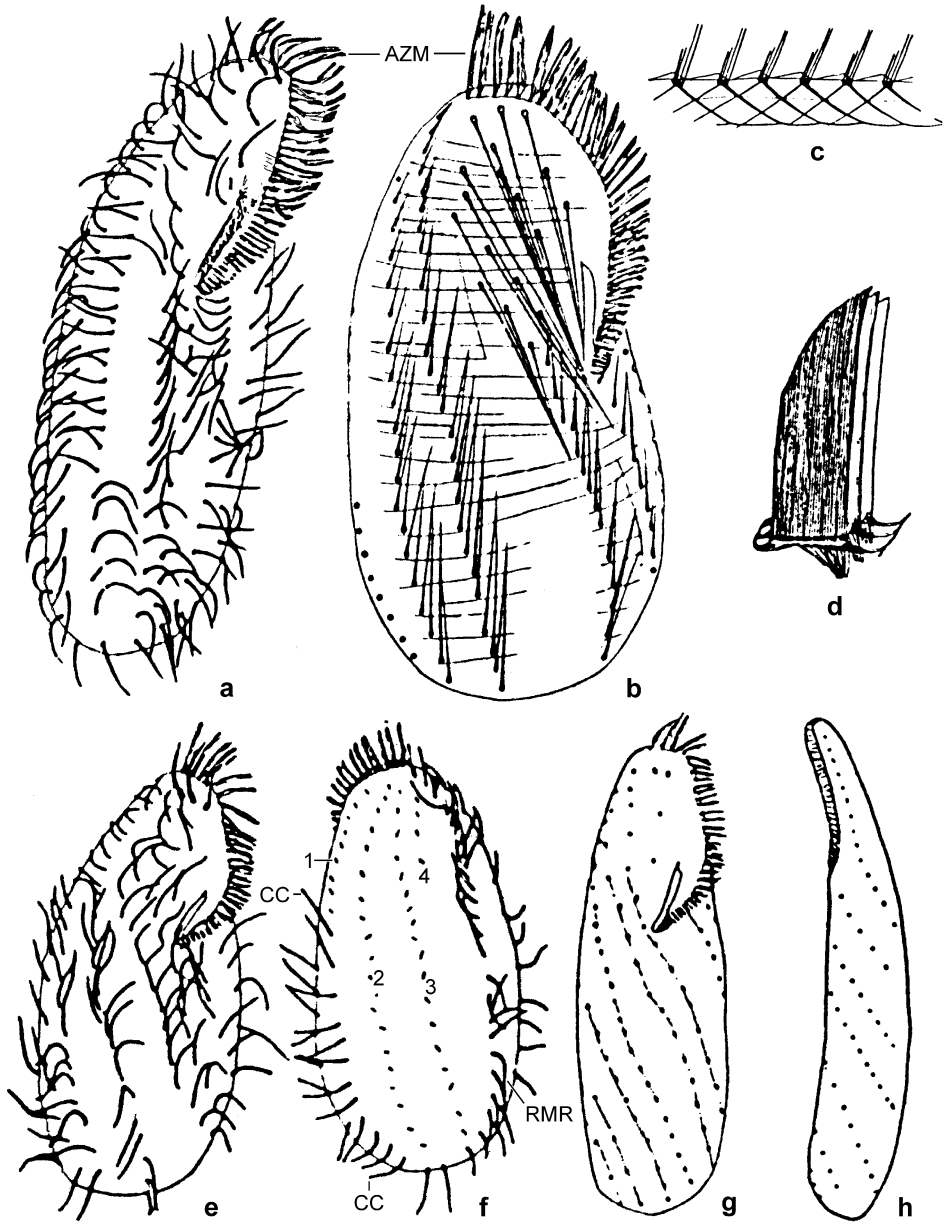


Fig. 67a–h *Kahliella simplex* (from Horváth 1934. a, e–h, Gentiana-violet staining; b, Malory-staining; c, d, other stainings). **a, b, e:** Infraciliature of ventral side. **c, d:** Details of adoral zone of membranelles. **f:** Infraciliature of dorsal side. Note that this pattern matches perfectly that of the other *K. simplex* populations (cp. with Fig. 65g, o, 66b, 70c). **g, h:** Cirral pattern of slightly twisted specimens. AZM = adoral zone of membranelles, CC = caudal cirri on dorsal kinety 1, RMR = right marginal row, 1–4 = dorsal kineties. Page 367.

pasture near the village of Seekirchen, about 10 km northeast of the city of Salzburg, Austria (Berger & Foissner 1987, p. 194). Both sites are in Central Europe, only about 700 km apart, and terrestrial.

(vii) Four slides of the population investigated by Berger & Foissner (1987) have been deposited in the Oberösterreichische Landesmuseum (= Upper Austrian Museum) in Linz (Aescht 2003, p. 396; 2008, p. 178). They have the accession numbers 1986/57–60. The neotype specimen illustrated is on the slide originally designated "P52".

Remarks: As already mentioned in the nomenclature section, the original description of *Kahliella simplex* is in Hungarian without English or German summary, making the paper unreadable for me. Consequently, the data presented below about this population are from the original illustrations (Fig. 67a–h) and other papers by Horváth. For example, the sample site of the type population is briefly described in a German-written paper about the physiology of *K. simplex* (Horváth 1936). As mentioned in the neotypification section above, the Austrian population (= neotype) of *K. simplex* described by Berger & Foissner (1987; Fig. 65a–g) matches perfectly the original description (Fig. 67a–h).

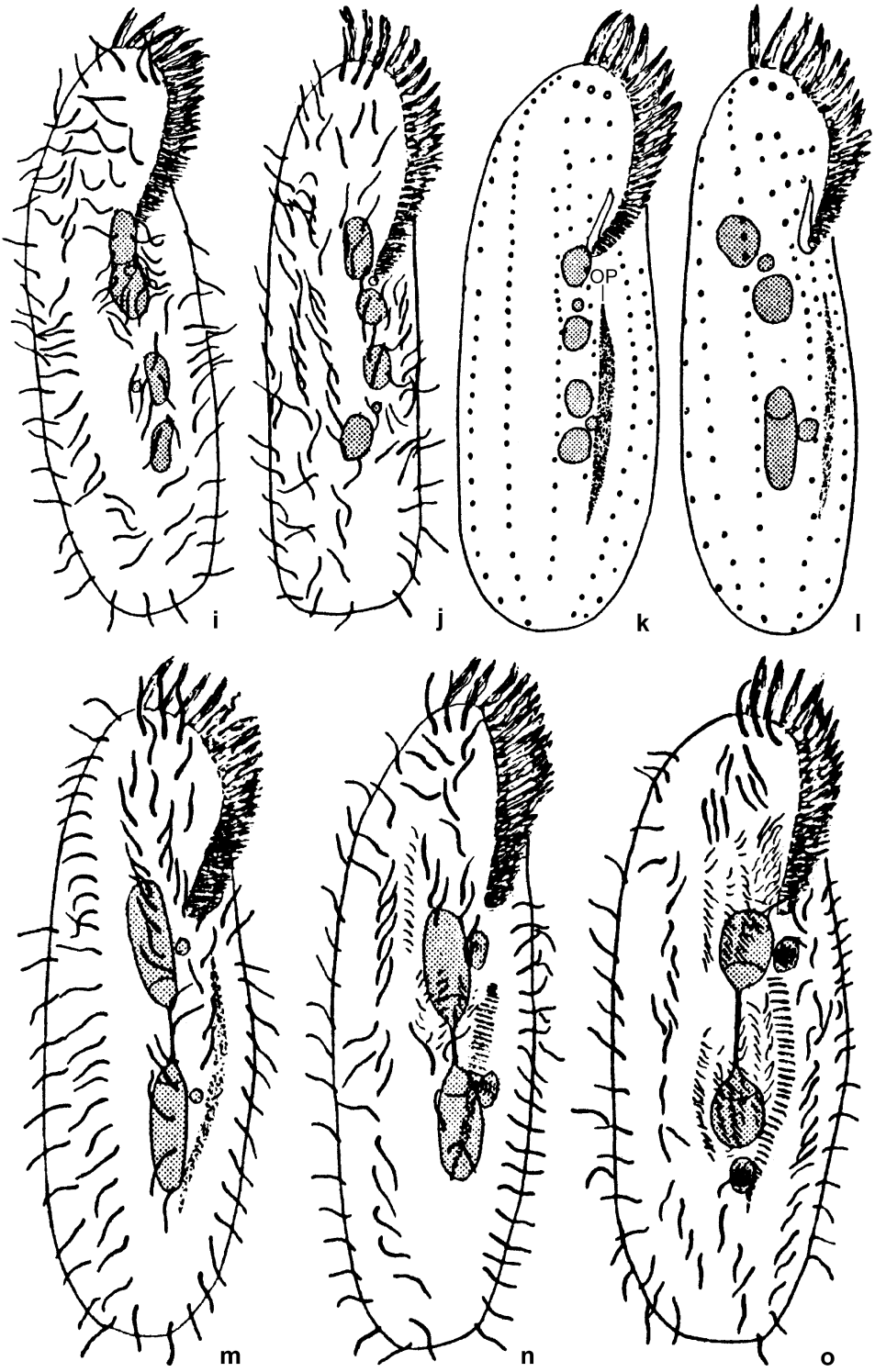
It cannot be excluded that *K. simplex* is the junior synonym of *K. acrobates*. For a detailed explanation of the situation and of the synonymy of *K. multiseta* Dragesco, 1970, see same chapter at *K. acrobates*. As a first step to solve the tricky situation, the population described by Berger & Foissner (1987) is fixed as neotype of *K. simplex* in the present review (see previous chapter).

The illustrations of *K. multiseta* from Africa provided by Dragesco (1970) are not very exact so that it is difficult to recognise the identity with *K. simplex*. However, Dragesco & Dragesco-Kernéis (1986) provided more detailed illustrations of the ventral and dorsal infraciliature of a French population so that the synonymy of these two species is beyond reasonable doubt.

Fleury & Fryd-Versavel (1982) did not identify their population, that is, designated it as *Kahliella* sp. Fleury et al. (1985) identified their population – which is obviously from the same site as the "*Kahliella* sp." of Fleury & Fryd-Versavel (1983) – as *K. acrobates*. However, since the dorsal infraciliature agrees very well with that described for *K. simplex*, I assign the French population to the present species (Fig. 65g, 66b). Likely, Fig. 4c of "*Kahliella bacilliformis* Gelei, 1954" in Fleury & Fryd-Versavel (1984) also shows *K. simplex* (see *Deviata*, p. 555).

Morphology (Fig. 65a–o, 66a, b, 67a–j, s, Table 22): At first the neotype population studied by Berger & Foissner (1987) is described (Fig. 65a–g). Then supplementary and/or deviating data from the other populations are mentioned.

Body size of neotype population investigated by Berger & Foissner (1987) about 110–160 × 50–70 µm in life; length:width ratio about 2.6:1 in protargol preparations (Table 22). Body outline elliptical, but sometimes also with parallel margins; both ends broadly rounded. Body about 2:1 dorsoventrally flattened (Fig. 65a–c). Macronuclear nodules in or slightly left of median, connected by a fine thread. Length to width ratio of rear macronuclear nodule 2.3:1 on average after protargol impregna-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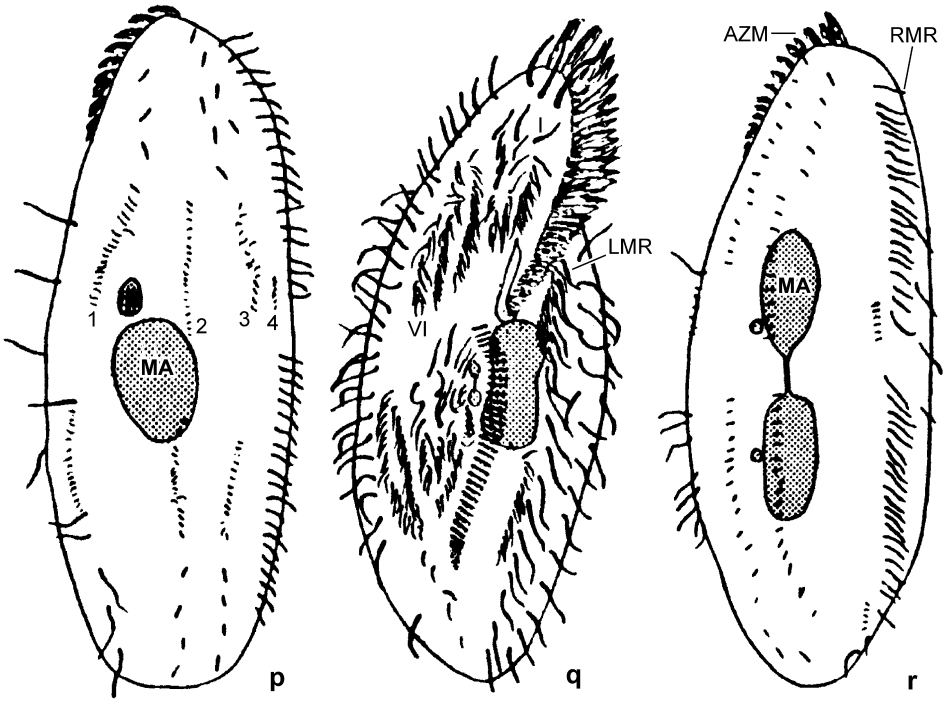
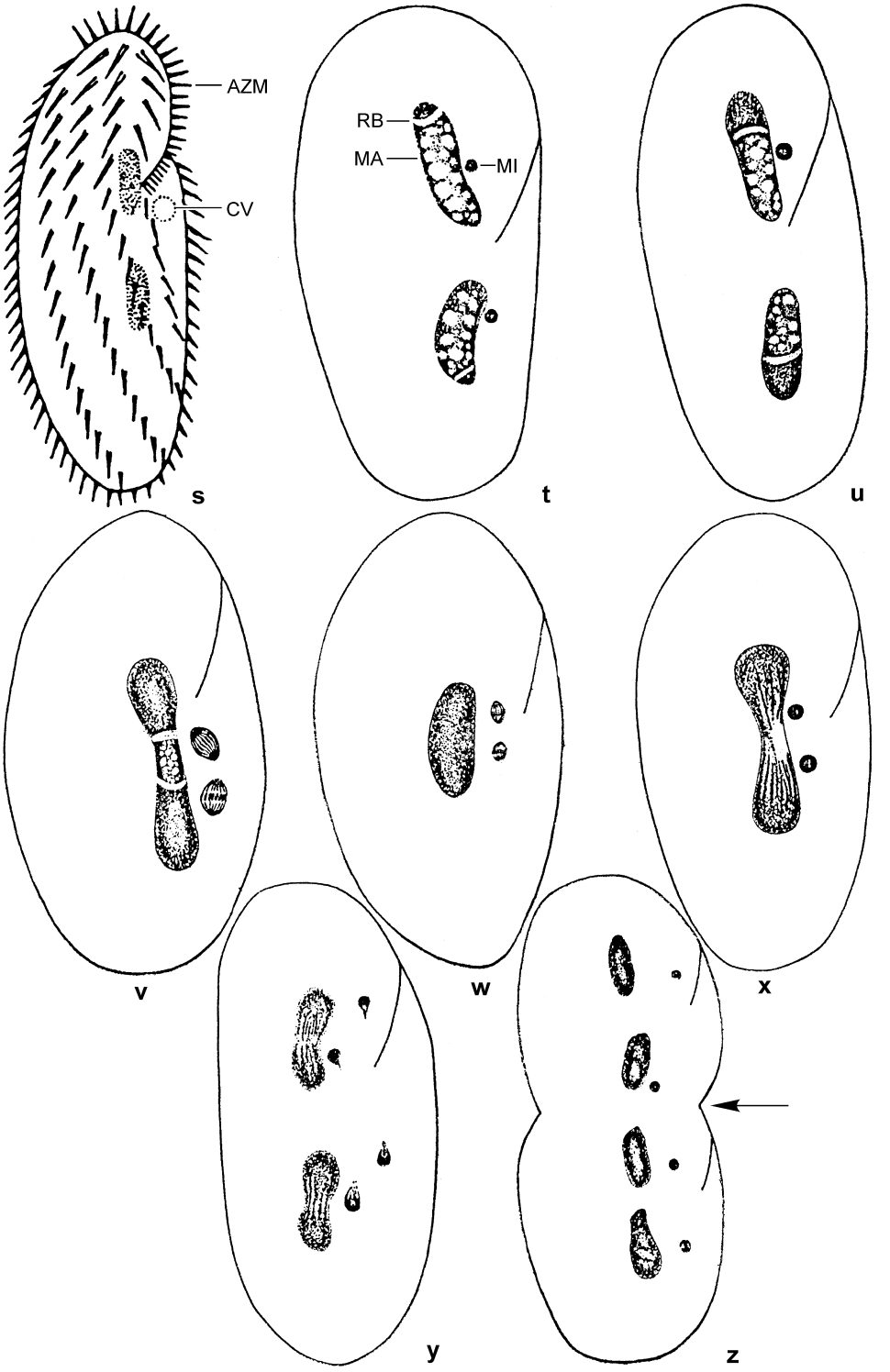


Fig. 67p–r *Kahliella simplex* (from Horváth 1936. p, Gentiana-violet staining; q, r, Malory-staining). Infraciliature of dorsal (p, r) and ventral (q) side of late dividers, size almost 200 µm. AZM = adoral zone of membranelles, LMR = left marginal row, MA = macronucleus, RMR = right marginal row, 1–4 = dorsal kineties (kinety 4 is a dorsomarginal row originating from/near the anterior end of the right marginal row primordium). Page 367.

tion (Fig. 65a, g, Table 22). Micronucleus/micronuclei close to macronuclear nodules. Contractile vacuole, as is usual, near left body margin about in middle of cell; during diastole sometimes with an anterior collecting canal (Fig. 65a, b). Cortical granules (designated as subpellicular granules by Berger & Foissner 1987) inconspicuous because less than 1 µm across, colourless, and arranged in loose rows; sometimes difficult to recognise and easily confused with the many subcortical mitochondria (1–3 µm) which make cells conspicuously brownish (Fig. 65e). Cytoplasm strongly viscid, with numerous yellow shining, 2–5 µm large crystals in posterior portion of cell and voluminous food vacuoles (Fig. 65a, e). Movement moderately rapid, usually creeping, sometimes freely swimming under rotation abound main axis of cell.

← **Fig. 67i–o** *Kahliella simplex* (from Horváth 1936. i–k, o, Gentiana-violet staining; l–n, Malory-staining). Infraciliature of ventral side and nuclear apparatus of very early to late dividers, size almost 200 µm. Note that the two macronuclear nodules of this population divide prior to cell division (i–l). For a detailed description of cell division see Fig. 70a–o. OP = oral primordium. Page 367.


AZM
CV
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Adoral zone occupies about 36% of body length on average (Table 22), shaped as in *Gonostomum*, that is, distal end in midline of anterior cell end, middle portion straight and extending along left cell margin, while proximal portion abruptly bent towards body centre; on average composed of 36 membranelles of ordinary fine structure. Paroral and endoral commence about at same level; paroral, however, only about one third of length of endoral; both membranes composed of narrowly spaced basal bodies/cilia. Buccal cavity small, covered by buccal lip. Cytopharynx extends obliquely backwards.

Cirral pattern of usual kahliellid variability (Table 22). All cirri about 20 µm long and thin, except for that in frontal area, which are slightly enlarged. Frontal cirri inconspicuous, left cirrus slightly behind level of middle and right cirrus, which is at distal end of adoral zone (Fig. 65f). Frontoventral row II (= buccal cirral row) composed of 2–3 cirri (middle frontal cirrus not included), rearmost cirrus near anterior end of undulating membranes indicating that this cirrus is homologous to cirrus II/2 (= buccal cirrus) of other hypotrichs (e.g., Berger 1999, p. 16; Berger 2006a, p. 2). Frontoventral row III (= parabuccal row) composed of 3–5 cirri, only slightly longer than row II. Frontoventral row IV commences slightly behind anterior body end (at about 8% of body length in specimen shown in Fig. 65f), extends inconspicuously sigmoidally, slightly to distinctly behind mid-body. Frontoventral row V commences somewhat ahead of level of proximal end of adoral zone, terminates near rear cell end (90% of body length in specimen shown in Fig. 65f). Frontoventral row VI begins near distal end of adoral zone, slightly curved, extends – distinctly set off from right body margin – to near rear body end. Right marginal row on dorsolateral side, commences about at level of frontal cirri, terminates roughly at cell end. Left marginal row com-

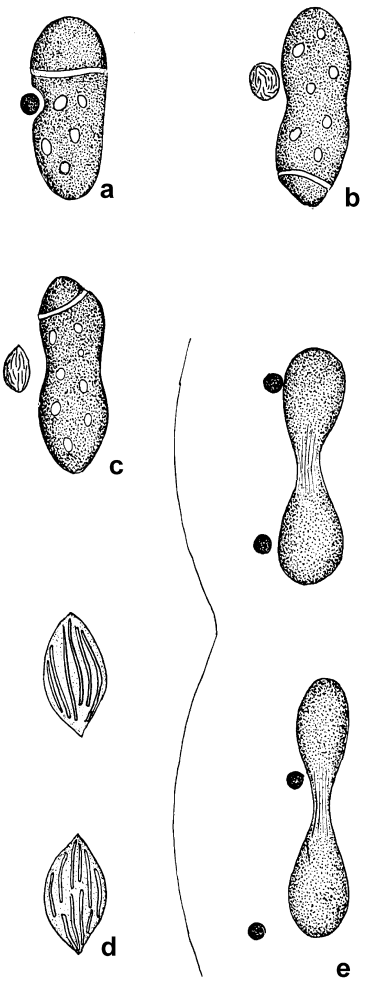


Fig. 68a–e *Kahliella simplex* (from Dragesco 1970. Feulgen stain). Division of nuclear apparatus, length of nodule shown in (b) is 23 µm. Page 367.

← **Fig. 67s–z** *Kahliella simplex* (s, from Stout 1954; t–z, from Ördögh 1960. s, from life?; t–z, carmine-aceto-acid staining). **s:** Ventral view, 140 µm. Size of cirri slightly exaggerated. **t–z:** Division of nuclear apparatus, t = 152 µm. Arrow in (z) marks division furrow. AZM = adoral zone of membranelles, CV = contractile vacuole, MA = macronuclear nodule, MI = micronucleus, RB = replication band. Page 367.

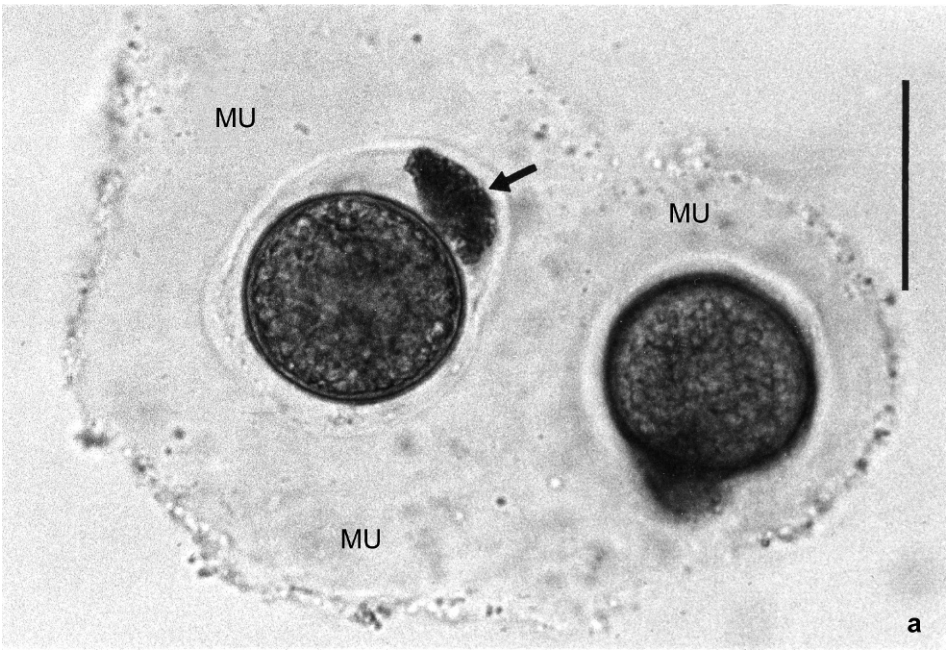
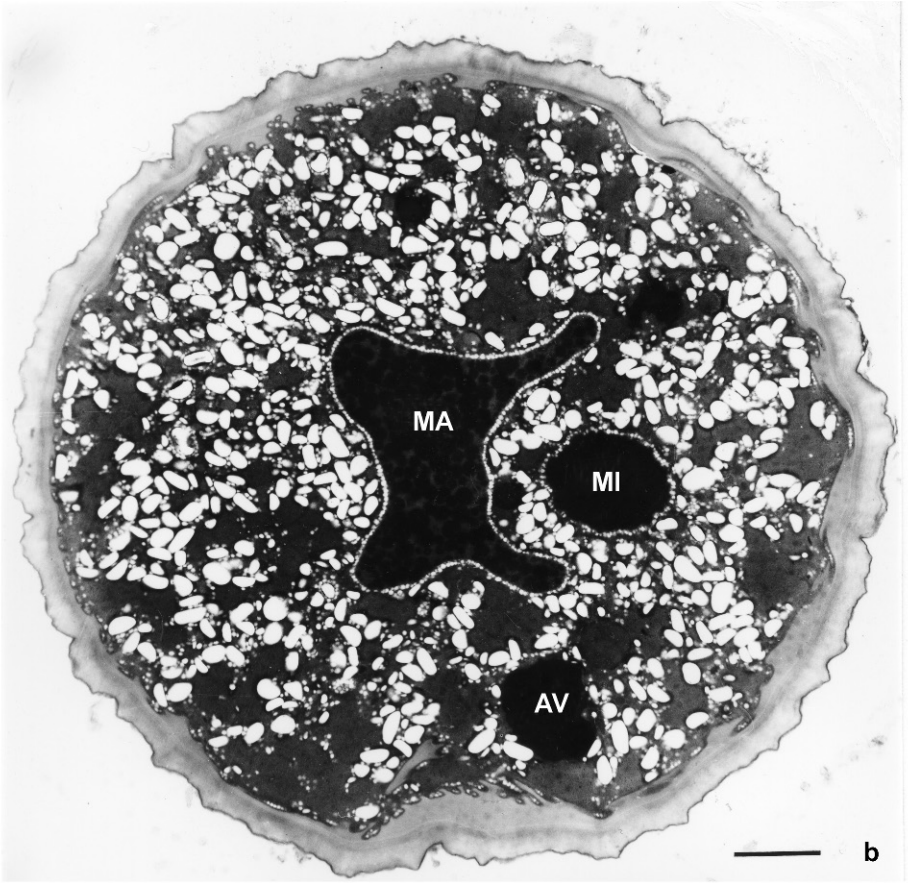


Fig. 69a *Kahliella simplex* (from Foissner & Foissner 1987. Bright field micrograph). Two resting cysts covered by a mucous layer. Arrow marks an agglomeration of crystal-like particles. MU = mucus. Bar = 40 µm. Page 367.

mences left of proximal end of adoral zone, terminates slightly to distinctly ahead of rear body end (at about 96% of body length in specimen shown in Fig. 65f); distance between individual cirri becomes wider from anterior to posterior. Between frontoventral row VI and right marginal row and between left marginal row and dorsal kinety 1 each 2–3 cirral rows, which are remnants of the frontoventral row VI, respectively, the left marginal row of the previous 2–3 generations. Thus, the distance between the individual cirri within these parental rows becomes wider and the number of cirri per row decreases from inside to outside. Total number of cirral rows (frontoventral rows, remnants of previous generations, marginal rows) rather constant (invariable 11 [dorsal kinety 1 included] in 19 specimens investigated by Berger & Foissner 1987).

Dorsal cilia about 3 µm long in life, invariably arranged in four kineties (Fig. 65g, Table 22). Anterior portion of kinety 1 (= leftmost kinety) composed of cilia, posterior portion composed of 8–13 cirri, which are designated as caudal cirri. Kine-

Fig. 69b, c *Kahliella simplex* (from Foissner & Foissner 1987. Transmission electron microscopic micrographs). **b:** Cross section of resting cyst, bar = 4 µm. **c:** Cyst wall with bacterium trapped between mucus and ectocyst, bar = 400 nm. AV = autophagous vacuole, EC = ectocyst, EN = endocyst, GL = granular layer, MA = macronuclear nodule, ME = mesocyst, MI = micronucleus, MU = mucus. Page 367. →


MA
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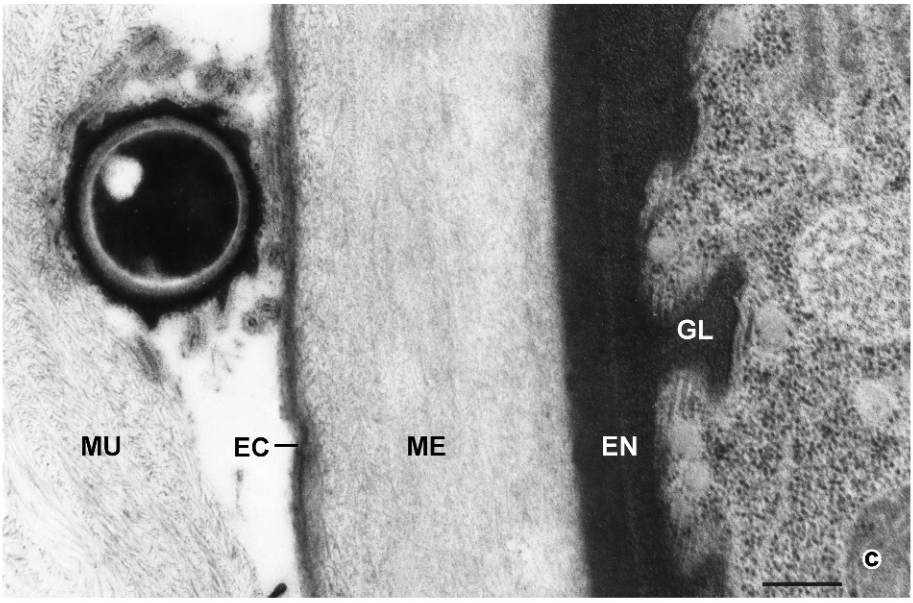
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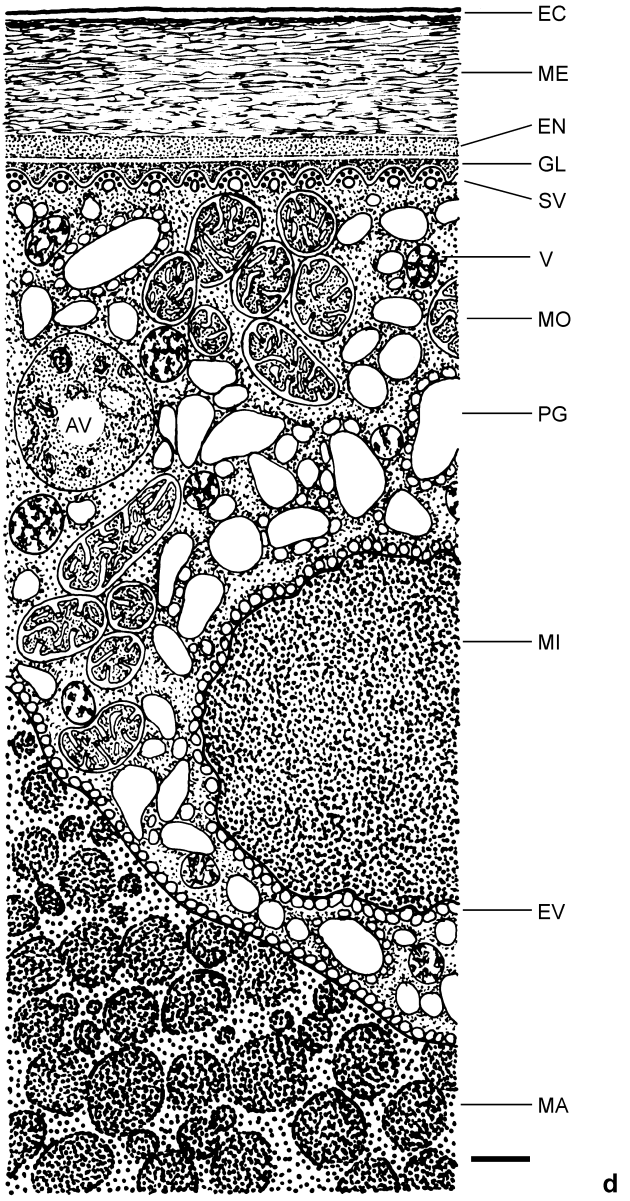


Fig. 69d *Kahliella simplex* (from Foissner & Foissner 1987). Schematic representation of ultrastructure of resting cyst, bar = 500 nm. For detail description, see text. EC = ectocyst, EN = endocyst, EV = epinuclear vesicles, GL = granular layer, MA = macronucleus, ME = mesocyst, MI = micronucleus, MO = mitochondrium, PG = paraglycogen granule, SV = subpellicular vesicles, V = vacuole with fuzzy content. Page 367.

ties 2 and 3 more or less distinctly shortened anteriorly, extend almost to rear cell end and lack caudal cirri. Kinety 4 (= dorsomarginal kinety) left of anterior portion of right marginal row, terminates at 26% of body length in specimen shown in Figure 65g. Frequently 1–2 basal body pairs ahead of the parental row left of dorsal kinety 1; probably, this is a remnant of the previous generation (Fig. 65g, arrow).

Additional and/or deviating observations from other populations: population studied by Eigner (1995) very similar to that described above (for differences see Table 22). The most important difference is an additional frontoventral row (row I6 in Eigner 1995 = frontoventral row Va in present review), which occurred in two thirds of the specimens studied morphometrically by Eigner (1995). Body length of fixed specimens of Yaounde population 55–90 µm, body size of Cotonou population 78–102 × 24–40 µm (mean = 88 × 33 µm; n = 13; Dragesco 1970, Dragesco & Dragesco-Kernéis 1986). Macronuclear nodules 12–25 µm (Yaounde population) and 13–18 µm (mean = 15 µm; n = 21; Cotonou population) long, respectively; 1–3 micronuclei 1.8–2.4 µm across (Cotonou population; Dragesco & Dragesco-Kernéis 1986). The population described by Horváth (1934) matches almost perfectly the neotype. For example, the average number of cirri in frontoventral row VI is 31 in the neotype (Table 22) and about 30 in the specimen shown in Fig. 67a. Thus, the reader is referred to Fig. 67a–h. Horváth (1939) found 2–4 micronuclei, even in clones. However, only one micronucleus divided mitotically. Horváth (1948a) described two methods to get amicronucleate specimens, namely by ultraviolet radiation and by metabolic products of *Azotobacter* sp. Amicronucleate specimens did not differ from normal specimens in morphology, movement, nutrition, digestion, excretion, and division (Horváth 1947). In addition, Horváth found that (i) the life-span was "interminable" (1800 generations and more) under optimal conditions, and (ii) the specimens were able to do endomixis and conjugation. In a later paper, he reported on hereditary tumour formation (Horváth 1950c).

Resting cyst (Fig. 69a–d): The cyst of *Kahliella simplex* was studied in detail by Foissner & Foissner (1987; for review see Gutiérrez et al. 1998, p. 99). It is spherical, has a diameter of 41.4 µm on average (SD = 2.6; SE = 0.5; CV = 6.3%; n = 22), a smooth surface, a coarsely granular cytoplasm, and is covered by a mucilaginous layer (up to 40 µm thick) often joining two or more cysts. Mucus fragile and sticky (thus cysts often adhere to substrate), slightly detached from cyst wall, inner border appears more refractive than periphery. Space between cyst wall and mucus contains an agglomeration of almost spherical, crystal-like particles (about 1.4 µm across) which were formerly inside the cytoplasm of pre-cystic stages (Fig. 69a). Such a granule agglomeration was already described by Grandori & Grandori (1934, their Fig. XXXIV C) and by Fauré-Fremiet (1957, p. 106) for *K. acrobates*. Interestingly, these particles disappear during the electron microscopical procedure (Foissner & Foissner 1987). Bacteria frequently on or inside the mucus. Wall yellowish, about 1.5 µm thick. Cyst volume is about 20% of the vegetative cell volume (Foissner & Foissner 1987; Foissner et al. 2006, p. 335).

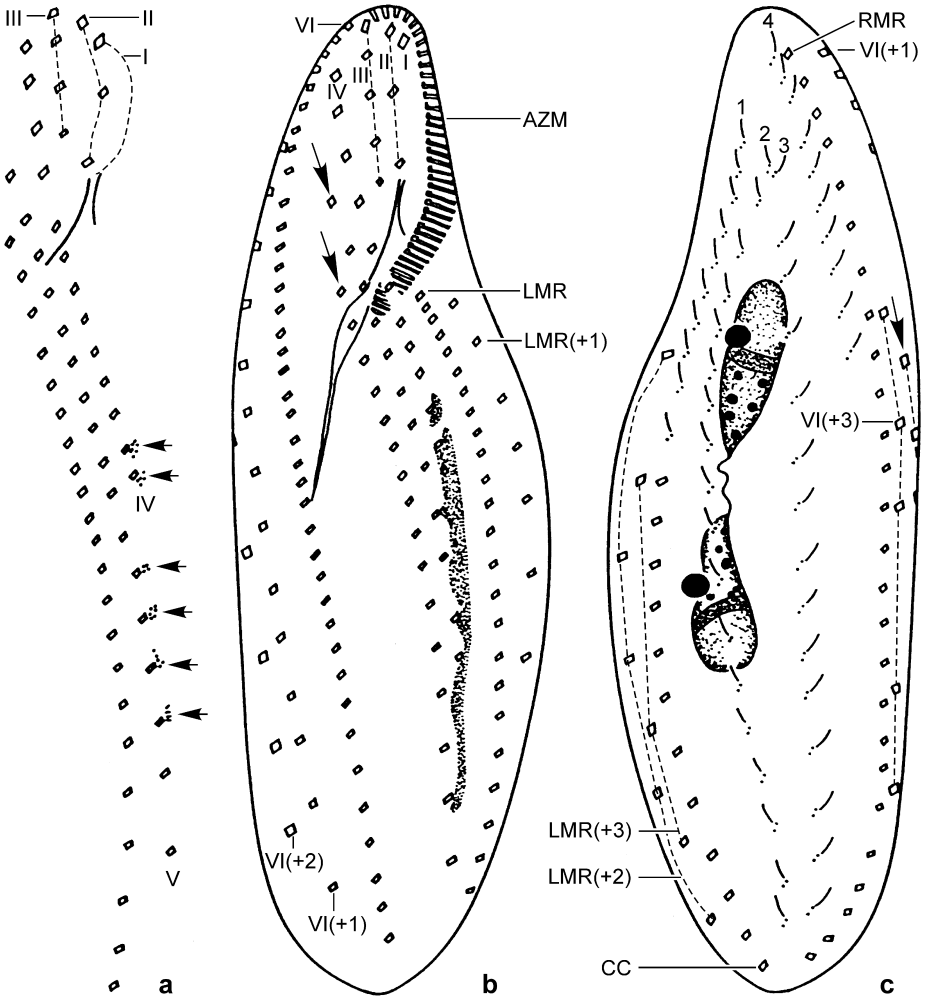


Fig. 70a–c *Kahliella simplex* (from Eigner 1995. Protargol impregnation). Broken lines connect cirri which originated from same anlage. **a:** Very early divider commencing with the formation of the oral primordium (arrows), 148 µm. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of a very early divider, 154 µm. One of the two rows marked with an arrow (b) is an additional frontoventral row V. Arrow in (c) marks the parental frontoventral row VI(+2). AZM = adoral zone of membranelles, CC = rearmost caudal cirrus, LMR = left marginal row, LMR(+1), LMR(+2), LMR(+3) = left marginal rows of previous generations, RMR = right marginal row, I–VI = frontoventral rows, VI(+1), VI(+2), VI(+3) = frontoventral row VI of previous generations, 1–4 = dorsal kineties (kinety 4 is a dorsomarginal kinety). Page 367.

For a complete description of the ultrastructure of the cyst, see Foissner & Foissner (1987). Here only some details are provided (Fig. 69b–d): macronuclear nodules fused to lobed mass (diameter up to 17 µm) and arranged in cyst centre; micronucleus about 5 µm across, appears uniformly fibro-granular, surface irregularly granu-

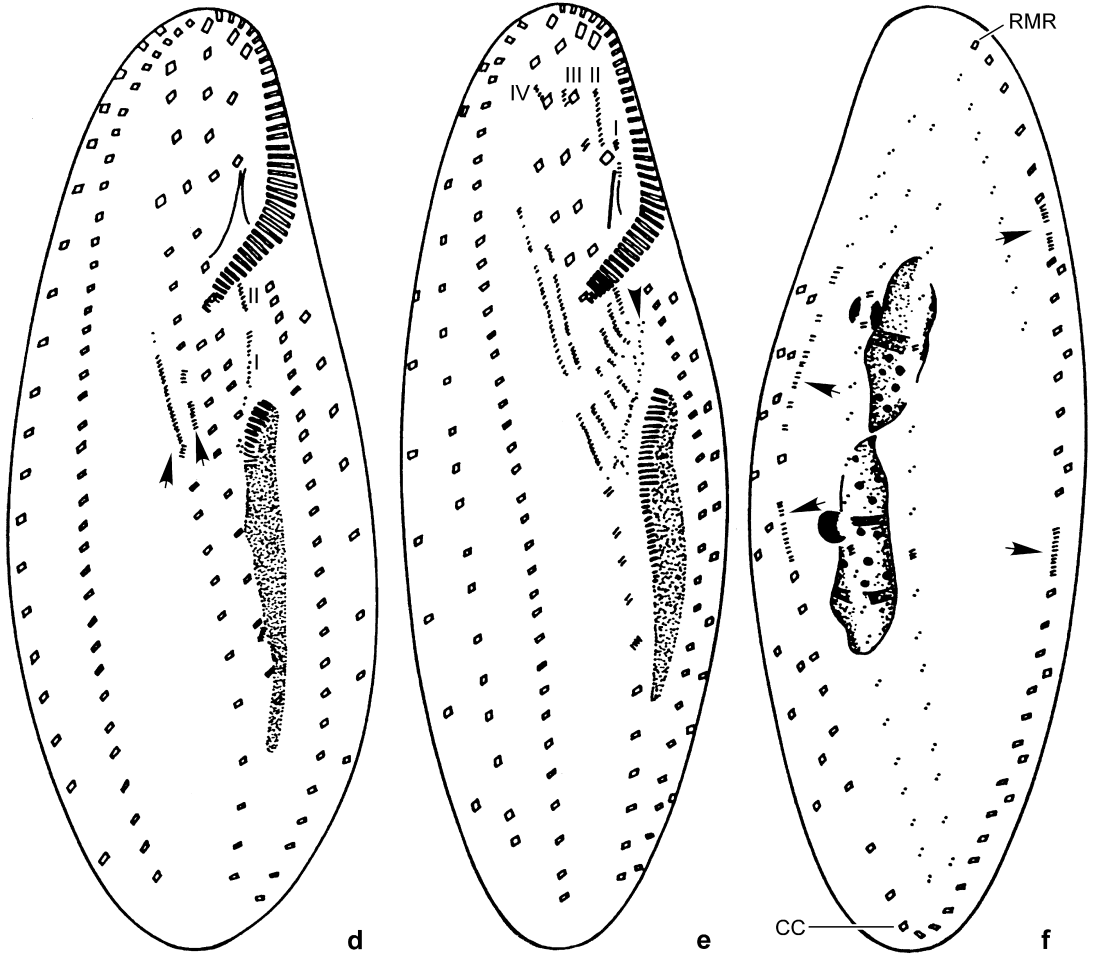


Fig. 70d–f *Kahliella simplex* (from Eigner 1995. Protargol impregnation). **d:** Infraciliature of ventral side of an early divider, 151 µm. Arrows mark anlagen V and VI. **e, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of a middle divider, 144 µm. Arrowhead marks the undulating membrane anlage. Note that in the opisthe seven frontoventral anlagen are formed (provided that the anlage right of the undulating membrane anlage [arrowhead] is the left frontal cirrus). Arrows in (f) mark the anlagen in the right marginal row and dorsal kinety 1. CC = caudal cirri on dorsal kinety 1, RMR = right marginal row, I–IV = frontal-ventral cirri anlagen. Page 367.

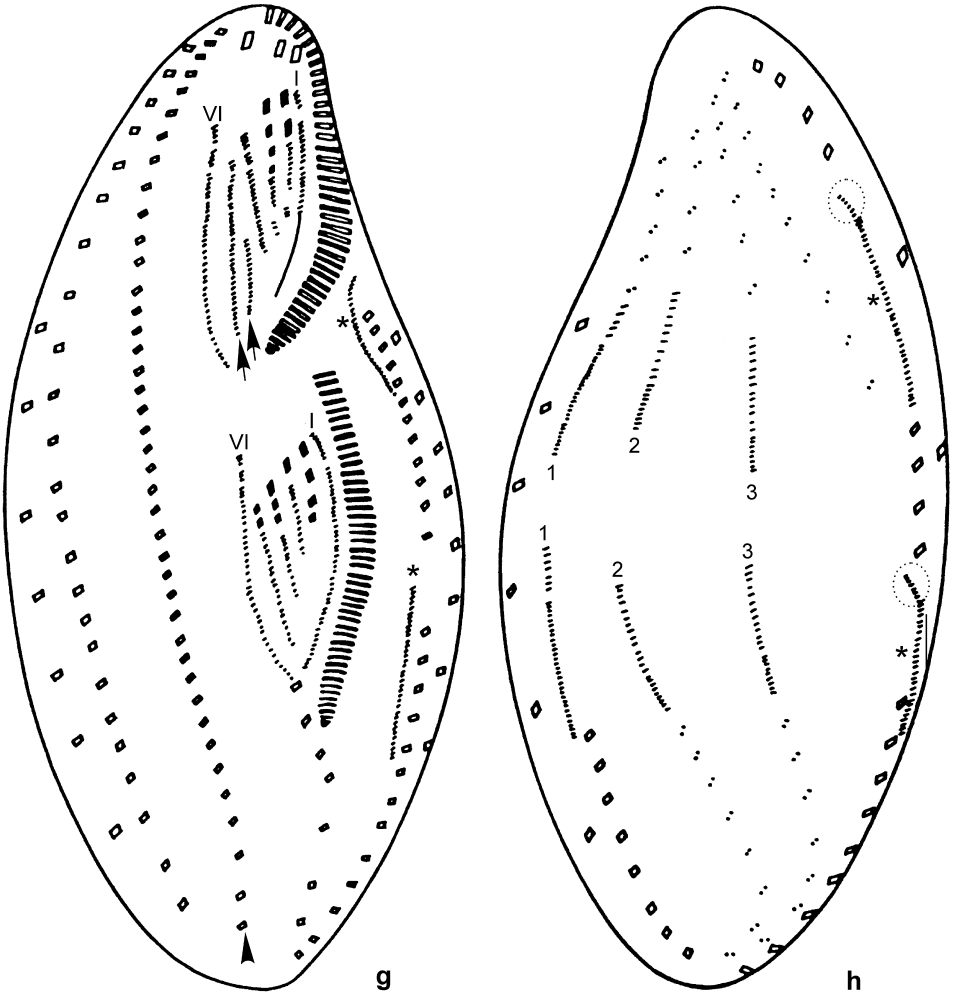


Fig. 70g, h *Kahliella simplex* (from Eigner 1995. Protargol impregnation). Infraciliature of ventral and dorsal side of a late divider, 132 µm. Arrowhead in (g) marks parental frontoventral row VI (does not participate in anlagen formation). One of the two anlagen of the proter marked by an arrow is supernumerary; by contrast, in the opisthe the ordinary number of six frontoventral cirral anlagen is formed. Asterisks mark anlagen for left marginal rows (g), respectively, right marginal rows (h). New dorsal kineties 4 are formed at/near anterior end of right marginal row anlagen (dotted circles). I, VI = frontoventral row anlagen, 1–3 = new dorsal kineties. Parental structures white, new black. Page 367.

lated. Macronucleus and micronucleus densely covered by vesicles (about 150 nm across) of low electron density. Cyst wall composed of (i) an inner granular layer; (ii) an endocyst about 170 nm thick; (iii) a filamentous mesocyst (0.8–1.0 µm thick); and (iv) a thin ectocyst (Fig. 69c, d). The ectocyst of *Kahliella simplex* is as thin as that of *Meseres corlissi*. However, it is composed of a membranous sheet in *Kahli-*

ella simplex, while coarsely granular in *Meseres* (Foissner 2005, Foissner & Pichler 2006).

For a brief discussion of the cyst-infection by a fungi, see chapter 4 in the general section.

Cell division (Fig. 67k–r, t–z, 68a–e, 70a–o): This part of the life cycle is described by Horváth (1936), Fleury & Fryd-Versavel (1982), and Eigner (1995). The formation of the frontoventral anlagen in *Kahliella simplex* is a rather complex process. Thus, a detailed analysis is difficult. In addition, the population studied by Eigner (1995) shows a variability in the number of frontoventral rows making the elucidation of the process still more difficult. Anyhow, the major goal of the analysis should be to homologise structures and processes occurring in *K. simplex* with those of other taxa, for example, the oxytrichids. Thus, in the paragraphs below only some features of the cell division are reviewed. For a more detailed description, see Eigner (1995).

Stomatogenesis begins with the formation of basal body fields left of the posterior portions of the frontoventral rows IV and V (Fig. 70a). These patches form, as is usual, a longitudinal oral primordium right of the left marginal row and the formation of adoral membranelles proceeds from anterior to posterior (Fig. 67k–m, 70b, d, e). The parental adoral zone is not or only indistinctly modified/reorganised during division, as is usual for the bulk of the hypotrichs.

The frontoventral cirri of *Kahliella simplex* basically originate from six frontalventral anlagen. Six anlagen are an old feature already present in the ground pattern of the hypotrichs (Berger 2007, 2008, 2008a). However, in some *Kahliella simplex* specimen/populations seven anlagen can occur. Figure 70g shows a specimen where the proter produces seven streaks, whereas in the opisthe the ordinary number of six anlagen is formed. Because of the high number of cirri in *K. simplex* it is difficult to say from which parental structure an anlage originates. However, the following statements can be made:

(i) Anlage I of the proter originates from/near the parental undulating membranes (Fig. 70e).

(ii) Anlage II of the proter originates from the cirrus between the middle frontal cirrus and the "buccal cirrus" (Fig. 70e). Later, the buccal cirrus obviously also contributes to the formation of this anlage (Fig. 70g).

(iii) Anlage III originates from the middle cirrus of the frontoventral row III (= parabuccal row; Fig. 70e), indicating that this cirrus is homologous to cirrus III/2 of the 18-cirri hypotrichs where this cirrus always produces anlage III of the proter (see Fig. 23 in Berger 1999).

(iv) Anlage IV is formed (initiated) from the second cirrus of frontoventral row IV (Fig. 70e) indicating that this cirrus is homologous to cirrus IV/3 of the oxytrichids and 18-cirri hypotrichs in general where it usually forms anlage IV of the proter (see Fig. 23 in Berger 1999).

(v) The two rightmost anlagen (that is, anlage V and VI in specimens with six frontoventral rows) for both the proter and the opisthe originate from an area in the

central portion of frontoventral row V (Fig. 70d). This strongly indicates that the few cirri involved are homologous to the cirri V/3 and V/4 of the 18-cirri hypotrichs/oxytrichids because they also form the anlagen V and VI of proter and opisthe (see Fig. 23c, d in Berger 1999).

(vi) Anlagen I and II of the opisthe originate, as in other hypotrichs, very likely from the oral primordium (Fig. 70d, e; Table 4 in Berger 1999). According to Eigner (1995), anlage III of the opisthe originates from disaggregating cirri of frontoventral rows IV and V. However, according to Table 4 in Berger (1999), the anlage III of the opisthe mostly (always?) originates from the oral primordium. From Fig. 70d and 70e it is basically impossible to find the exact origin of anlage III.

(vii) Anlage IV of the opisthe very likely originates from a postoral portion in frontoventral row IV (Fig. 70d, e), indicating that this region (likely only few cirri involved) is homologous to cirrus IV/2 of the 18-cirri hypotrichs/oxytrichids. In this group, cirrus IV/2 is usually responsible for the formation of anlage IV of the opisthe (see Fig. 23 in Berger 1999).

(viii) Frontoventral row VI is not involved in primordia formation showing that this row is homologous with the cirri VI/3 and VI/4 (= frontoterminal cirri) of the other hypotrichs because the cirri of the rightmost anlage (= anlage VI in the 18-cirri hypotrichs/oxytrichids) (almost) never contribute to anlagen formation.

(ix) The old/parental frontoventral row VI is retained in the next generation and shifted rightwards, that is, towards the cell margin (Fig. 70g, i). Up to three old rows are present whose number of cirri is, however, roughly halved each time due to the division process. Thus, these rows are easily recognisable by the their wide space between the individual cirri (e.g., Fig. 70f, g).

The right marginal row of *K. simplex* divides in the ordinary manner, that is, two anlagen occur within the parental row (Fig. 70f, h). During later stages the anlagen elongate and simultaneously parental right marginal cirri are resorbed and/or(?) involved in the anlagen formation. From (close to?) the anterior end of the anlagen, the dorsomarginal kinety (= dorsal kinety 4) is formed (Fig. 70h). Using this feature, the rightmost cirral row of *K. simplex* can be homologised unequivocally with the right marginal row of other hypotrichs. By contrast, Eigner (1995) did not use the term marginal row because "more than one long cirral row on each lateral side" is present. The two anlagen for the left marginal row develop right of the anterior (for proter) and middle (for opisthe) portion of the parental left marginal row (Fig. 70g). Obviously some parental marginal cirri are involved in primordia formation (Eigner 1995 termed this mode neokinetal 5). Interestingly, the parental left marginal row is not adsorbed, but is retained in the 2–3 next generations. Thus, between the left marginal row and dorsal kinety 1, two or three old left marginal rows – here designated as left marginal rows (+1) to (+3) – are present (Fig. 65f, g, 70b, c). The number of cirri per old row is of course roughly halved during each division (Table 22). After two or three generations, the outermost, old left marginal row disappears. Eigner (1995) introduced for this feature, which occurs in various taxa (e.g., *Engelmanniella*, p. 498; *Coniculostomum*, Berger 1999), the term neokinetal wave.

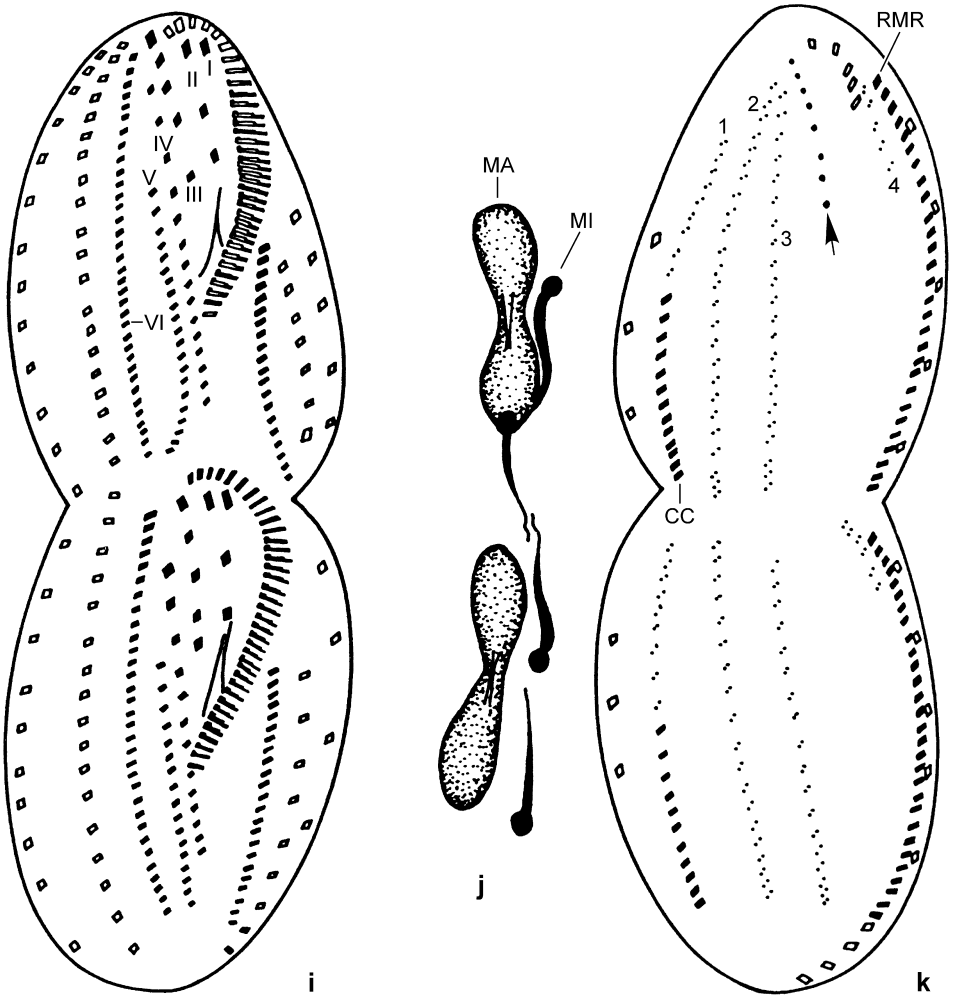


Fig. 70i–k *Kahliella simplex* (from Eigner 1995. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of a very late divider, 144 µm. The bristle row in (k) marked by an arrow is very likely the parental dorsal kinety 4. Parental structures white, new black. CC = rearmost caudal cirrus of proter, MA = macronuclear nodules, MI = micronucleus, RMR = right marginal row of proter, I–VI = frontoventral rows, 1–4 = dorsal kineties of proter (kinety 4 is a dorsomarginal kinety). Page 367.

The dorsal ciliature of *Kahliella simplex* is obviously in the *Urosomoida*-pattern (= type 2 in Foissner & Adam 1983a; for detailed explanation, see Berger 1999, p. 73), because the formation of this pattern proceeds as in *Urosomoida agiliformis* Foissner, 1982 (Foissner & Adam 1983b; for review see Berger 1999, p. 356).[1]

[1] *Urosomoida*, *Urosoma*, and some other 18-cirri hypotrichs previously classified in the oxytrichids (Berger 1999), are now classified rather vague as "non-oxytrichid Dorsomarginalia" because they lack the oxytrichid fragmentation of dorsal kinety 3 (Berger 2008, p. 46).

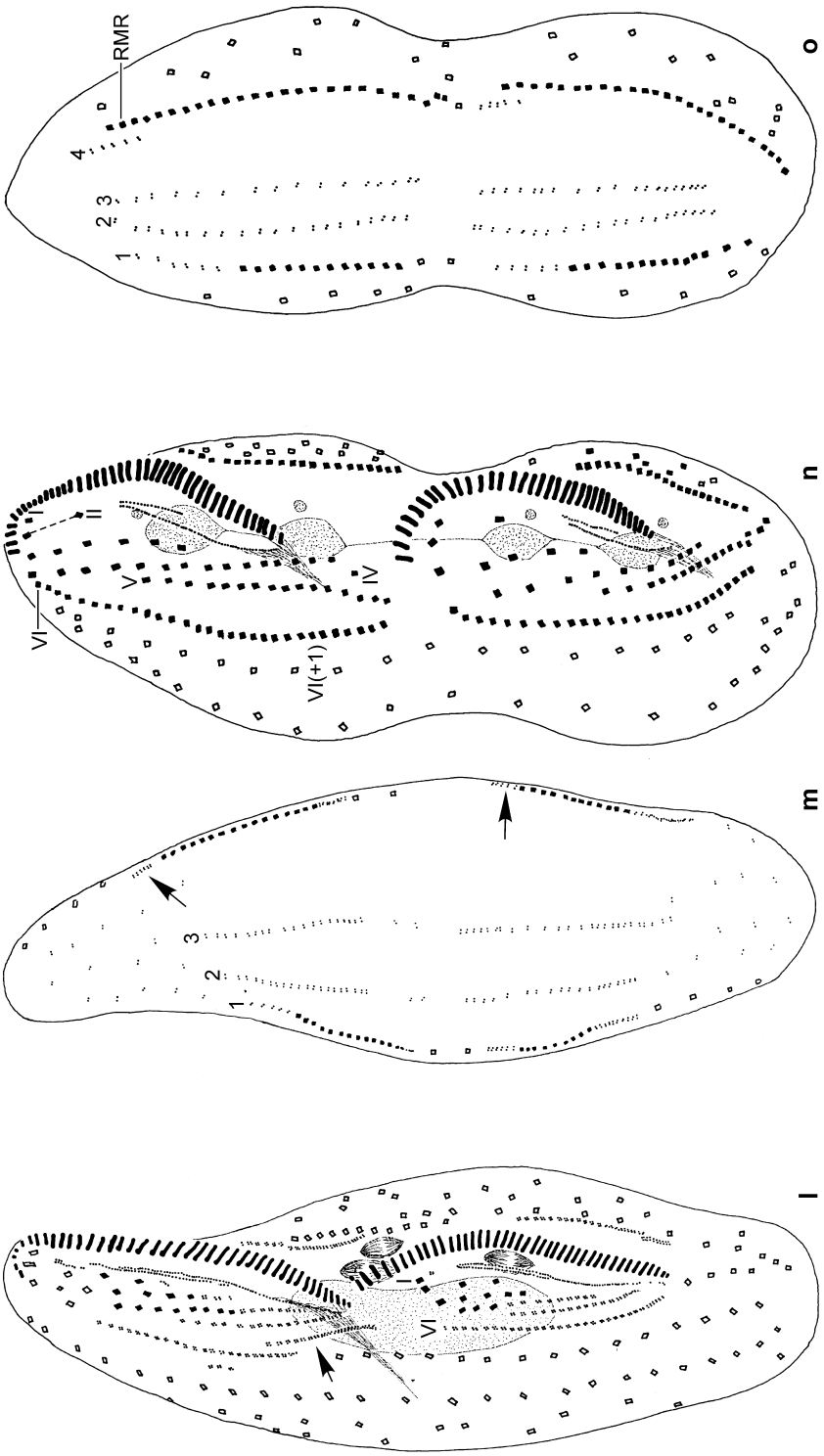


Fig. 70l–o *Kahliella simplex* (from Fleury & Fryd-Versavel 1982. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of a late (l, m; 158 µm) and a very late (n, o; 120 µm) divider. Arrow in (l) marks supernumerary frontal-ventral anlage, arrow in (m) denotes dorsomarginal kinety anlagen. Parental structures white, new black. I–VI = frontoventral anlagen/rows, RMR = new right marginal row of proter, VI(+1) = parental frontoventral row VI, 1–4 = dorsal kineties (kinety 4 is a dorsomarginal kinety). Page 367.

Briefly, each two anlagen originate within kineties 1–3 and kinety 4 is a dorsomarginal kinety because it originates from/near the anterior end of the right marginal row anlagen (Fig. 70h, k). An interesting feature of *K. simplex* and *K. acrobates* (Fig. 62e) is the high number of caudal cirri on dorsal kinety 1 (combined cirral row according to Eigner 1995). Kineties 2 and 3 do not form caudal cirri (Fig. 70f, h, k, m, o). The parental dorsal kinety 4 (arrow in Fig. 70k) is obviously resorbed in later stages because interphasic specimens have invariable four dorsal kineties (row with caudal cirri and dorsomarginal row included; Table 22).

The nuclear apparatus divides in the plesiomorphic mode (Fig. 67l–r, t–z, 68a–e, 70c, f, j, l, n). The two macronuclear nodules fuse to a single mass during early and middle stages. In late stages this row divides so that each filial product gets the species-specific number of two nodules. Usually, each nodule has one replication band; however, two bands per nodule were observed in several individuals indicating that these nodules, which are usually larger, are actually two nodules (Fig. 70f).

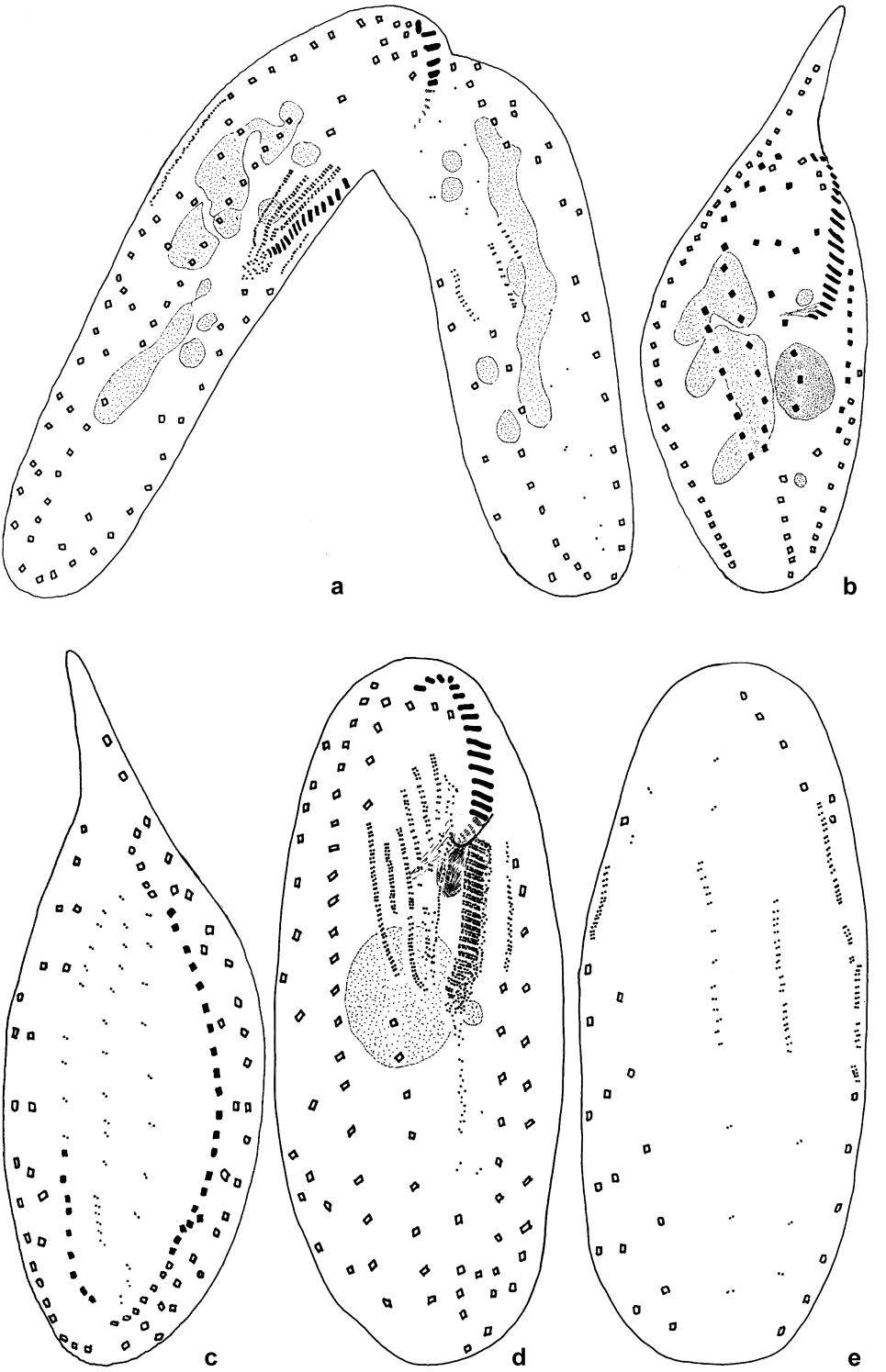
Ördögh (1960) found that the chromatin bodies (nucleoli) disappear when the replication band passes the macronucleus and reappear only in the daughter macronucleus (for review see Raikov 1969, p. 54).

Horváth (1950a) studied the reproduction of amicronucleate populations. The generation time of normal and amicronucleate specimens was identical at 24°C. By contrast, amicronucleate specimens reproduced faster than normal specimens at 34°C. Amicronucleates were killed by the drug proactinomycin, in contrast to micronucleates, which encysted (for review, see Ng 1986).

Conjugation and physiological reorganisation: Horváth (1948b) studied the conjugation of normal specimens and amicronucleate ones. Conjugation was triggered by a rapid increase of temperature. About 50% of the conjugation pairs consisted of a specimen with a normal nuclear apparatus and a specimen without micronuclei. Horváth (1952) described intraclonal conjugation (selfing). Rao (1966) studied conjugation in *Kahlia* sp. (isolated from a sewage sample in Bombay, India), with special references to meiosis and endomitosis. The micronuclei divided three times before synkaryon formation and two times thereafter. The morphogenetic processes during conjugation and physiological reorganisation have been described by Fleury & Fryd-Versavel (1982; Fig. 71a–g) and Fleury (1983, p. 159).

Ultrastructure: For a detailed description of the ultrastructure, see Fleury et al. (1985, 1985a). Just beneath the cell surface is a layer of longitudinal microtubules. Grimes (1972) and Wirnsberger-Aescht et al. (1989) found the same (similar?) situation in other flexible hypotrichs, namely *Oxytricha hymenostomata* (for review, see Berger 1999, p. 150) and *Engelmanniella mobilis* (p. 502). By contrast, in species of the *Stylonychia mytilus*-complex, which have a rigid cortex, two crosswise arranged layers are present (Puytorac et al. 1976).

Occurrence and ecology: *Kahliella simplex* prefers terrestrial habitats (Horváth 1950b p. 160; Foissner 1987a, p. 124; 1998, p. 204). Horváth (1934, p. 60) discovered *K. simplex* in the flower-garden of the University of Szeged (Szukováthy-Place) in Hungary. According to Horváth (1936, p. 482), the type species *K. acrobates* oc-


a
b
c
d
e

curred at the same site. Due to the neotypification (see above), the new type locality of *K. simplex* is the upper soil layer (0–5 cm) of a fertilised pasture ("Versuchsfläche E" in Foissner et al. 1987) near the village of Seekirchen (Salzburg), Austria (Berger & Foissner 1987; see also Foissner & Foissner 1988, p. 82); the population studied by Foissner & Foissner (1987) is from the same area.

Records substantiated by morphological data: old and dry birdnest under the roof of a stable in the village of Schrötten, Austria (Eigner 1995); puddle with *Euglena* bloom due to pollution with sewage sludge from the sewage treatment plant Eching, Bavaria, together with *Nudiamphisiella illuvialis* (W. Foissner, pers. comm.); soil(?) sample from near a dunghill in the region of the city of Troyes, France (Fleury & Fryd-Versavel 1982, Fleury et al. 1985).

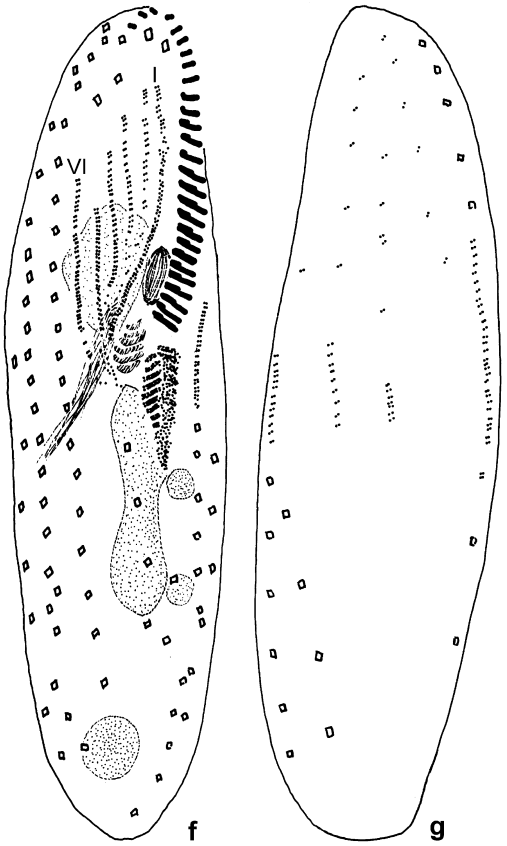


Fig. 71f, g *Kahliella simplex* (from Fleury & Fryd-Versavel 1982. Protargol impregnation). Physiological reorganisation, 121 µm. I, VI = frontal-ventral cirri anlagen. Page 367.

Records of *K. simplex* not substantiated by morphological data: sandy soil derived from the flood area of the river Tisza at the city of Szeged (Hungary) and garden soil from the same area (Horváth 1950b, p. 155, 156, 159); dry moss and adhering sandy soil (pH 6.4) from rocks in the surroundings of the Sheldrick waterfalls, Shimba Hills Nature Reserve (4°25'S 39°20'E), Kenya (Foissner 1999, p. 323). *Kahliella simplex* was not found during detailed surveys of Australian and Namibian soils (Blatterer & Foissner 1988, Foissner et al. 2002a).

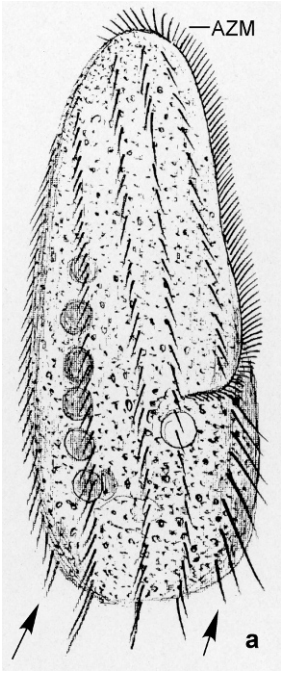
← **Fig. 71a–e** *Kahliella simplex* (from Fleury & Fryd-Versavel 1982. Protargol impregnation). Conjugation. **a:** Conjugating pair (113 µm) showing first reorganisation of ciliature and degeneration of the macronuclei. **b, c:** Infraciliature of ventral and dorsal side of one partner after separation, 90 µm. Note the reduced infraciliature (e.g., lacking undulating membranes). **d, e:** Infraciliature of ventral and dorsal side, 102 µm. Second reorganisation of infraciliature. Page 367.

Type locality of the synonym *Kahliella multiseta* is Yaounde, Cameroon (Dragesco 1970; see also Dragesco 1980, p. 183). Dragesco & Dragesco-Kernéis (1986) found it in Cotonou (Benin) and in Paris (France; French population studied by Fryd-Versavel). Records of the synonym not substantiated by morphological data: clean section of Manzanares River, La Pedriza, Madrid, Spain (Fernandez-Leborans & Novillo 1995, p. 31); with 12% dominance in a polluted section (10 µg l^{-1} cadmium, 1140 µg l^{-1} lead acid) of the Jarama River, Spain (Fernandez-Leborans & Novillo 1996, p. 315). The synonym is also mentioned in a comparative analysis of the ciliates of Azerbaijanian freshwater with that of other regions of the world (Alekperov 1986).

Kahliella simplex feeds on bacteria, diatoms, heterotrophic flagellates, autotrophic flagellates (*Polytoma*), and fungi (Horváth 1934, Berger & Foissner 1987, Foissner 1987a, p. 124). Biomass of 10^6 specimens about 157 mg (Foissner 1987a, p. 124; 1998, p. 204). Horváth (1950b, p. 160) found *K. simplex* in active condition in October and November, that is, during the cold season. However, in the laboratory it grew best at 25–30°C.

Incertae sedis in *Kahliella*

"New Genus" by Conn (1905)
(Fig. 72a)



1905 **New Genus** – Conn, Bull. Conn. St. geol. nat. Hist. Surv., 2: 58, Plate XXX, Fig. 279 (Fig. 72a; brief description; very likely no voucher slide available).

Remarks: Conn (1905) found two specimens and provided a short description and one illustration, which are presented only to complete the picture. The cirral pattern and the shape of the adoral zone are reminiscent of a kahliellid or gonostomatid, for example, *Kahliella* or *Wallackia*. It is provisionally assigned to *Kahliella* because (distinct) caudal cirri are obviously lacking. However, details of the description and the illustration must not be overinterpreted because Conn's (1905) observations are not of very high quality.

Morphology: Body size about 120 × 50 µm (estimated from illustration). Body outline elongate, anterior

Fig. 72a "New Genus" (from Conn 1905). Ventral view from life, 120 µm. Arrows mark marginal rows. AZM = adoral zone of membranelles. Page 396.

end rounded, posterior one almost truncated. Body not flexible (however, the general appearance does not indicate that it is a stylonychine and therefore rigid hypotrich). Four macronuclear nodules (this statement indicates that the six globules in the right body portion are not the macronucleus). Contractile vacuole immediately behind cytostome. Adoral zone large, that is, extending to 67% of body length (indicating that it is an early postdivider); zone kahliellid, respectively, gonostomatid, that is, most membranelles arranged along anterior and left anterior body margin and only proximal portion almost rectangularly curving rightwards. Four frontoventral rows, left one extending from anterior body end to proximal end of adoral zone, other rows of body length. Left marginal row short because commencing at proximal end of adoral zone, right one of body length. Transverse cirri obviously lacking. Dorsal infraciliature unknown; distinct caudal cirri obviously lacking.

Occurrence and ecology: Conn found two specimens in freshwater of Connecticut, USA, possibly in Middletown (Conn 1905, p. 10).

Parakahliella Berger, Foissner & Adam, 1985

1985 ***Parakahliella* nov. gen.**[1] – Berger, Foissner & Adam, Protistologica, 21: 309 (original description). Type species (by original designation): *Paraurostyla macrostoma* Foissner, 1982.

1987 ***Parakahliella* Berger, Foissner et Adam, 1985** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (classification of hypotrichs).

1989 ***Parakahliella*** [2] – Berger & Foissner, Bull. Br. Mus. nat. Hist. (Zool.), 55: 17 (improved diagnosis).

1994 ***Parakahliella* Berger et al., 1985** – Tuffrau & Fleury, Traite de Zoologie, 2: 137 (classification of hypotrichs).

1995 ***Parakahliella* Berger, Foissner and Adam, 1985** [3] – Eigner, Europ. J. Protistol., 31: 363 (improved diagnosis).

2001 ***Parakahliella* Berger, Foissner & Adam 1985** – Aescht, Denisia, 1: 116 (catalogue of generic names of ciliates).

2001 ***Parakahliella* Berger, Foissner and Adam, 1985** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 68 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).

2002 ***Parakahliella* Berger, Foissner and Adam, 1985** [4] – Lynn & Small, Ciliophora, p. 456 (guide to ciliate genera).

2007 ***Parakahliella* Berger, Foissner et Adam, 1985** – Jankowski, Ciliophora, p. 462 (revision of ciliates).

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[1] Berger et al. (1985) provided the following diagnosis: Kahliellidae with caudal cirri and more than one right and one left somatic ("marginal") cirral row. Some parts of the parental left somatic (marginal) infraciliature are preserved in the post-divider.

[2] Berger & Foissner (1989b) provided a slightly modified diagnosis: Kahliellidae with caudal cirri and 1 or more right and left marginal rows. During morphogenesis some parental dorsal rows are conserved as new kinety in the filial products.

[3] Eigner (1995) provided the following diagnosis: More than one long cirral row on right and left side of body. At least one of them is typically parental (old) on each side. One species has in only one out of fifty individuals more than one long cirral row on left side. Caudal cirri, dorsomarginal kinety and typically parental (old) dorsal kineties (wider spaced basal body pairs). Neokinetal wave to the left on both sides of adoral zone of membranelles.

[4] Lynn & Small (2002) provided the following characterisation: All midventral cirral files terminating removed from posterior end; transverse cirri, absent; caudal cirri, dorsal.

2008 ***Parakahliella* Berger, Foissner & Adam, 1985** – Lynn, Ciliated protozoa, p. 357 (revision of ciliates).

Nomenclature: No derivation of the name is given in the original description. *Parakahliella* is a composite of the prefix *para-* (closely related; Werner 1972) and the genus-group name *Kahliella* (see there for derivation). The name alludes to the resemblance of *P. macrostoma* and *Kahliella* species. Feminine gender because ending with *-ella* (ICZN 1999, Article 30.1.3). Name-bearing type of the Parakahliellidae Eigner, 1997 and its derivatives.

Parakahliella marina in Song (2004, p. 748) is likely an unintended combination of *Kahliella marina* and *Parakahliella* (see *Pseudokahliella marina*; p. 663).

Characterisation (A = supposed apomorphy): Kahliellidae(?). Adoral zone of membranelles formed like a question mark. Undulating membranes long, curved, and optically intersecting. Frontoventral cirri pattern relatively variable, basically composed of a buccal row, a parabuccal row, and two long frontoventral rows. Frontoventral cirri originate basically from five anlagen. Transverse cirri lacking. One or more right and one or more left marginal rows. Five dorsal kineties which originate (i) intrakinetally (kineties 1–3), (ii) by preservation of parental kineties 4 and 5 (kinety 4; A), and (iii) dorsomarginally (kinety 5). Caudal cirri at kineties 1 and 2. Terrestrial.

Additional characters: Body flexible, but not distinctly contractile; on average 6–10 macronuclear nodules left of midline; cortical granules lacking; parts of parental left marginal ciliature retained in *P. macrostoma* and *P. terricola*; dorsal cilia 2–5 µm long in life; perhaps confined to Europe/Eurasia.

Remarks: Originally, Foissner (1982) assigned *Parakahliella macrostoma* to *Paraurostyla* Borror, 1972, a genus classified in the oxytrichids on the basis of some features of the ventral morphogenesis (Borror 1979, Foissner 1982, Wirnsberger et al. 1985). Berger et al. (1985) demonstrated distinct differences in the cell division of *Paraurostyla macrostoma* and *P. weissei*, type of *Paraurostyla*. Consequently, we established *Parakahliella* to include *Paraurostyla macrostoma* (type) and the obviously closely related (synonymous?) *P. terricola*. The classification in a separate genus is indispensable, inter alia, because of distinct differences in the dorsal kinety pattern and formation: *Paraurostyla* has the characteristic oxytrichid kinety fragmentation (for review, see Berger 1999, p. 841), which is lacking in *Parakahliella*. Thus, *Paraurostyla* is a characteristic oxytrichid, while *Parakahliella* belongs to the non-oxytrichid Dorsomarginalia.

Berger et al. (1985) classified *Parakahliella* in the Kahliellidae because it met the diagnosis of the kahliellids, namely, meridionally arranged cirral rows and lacking transverse cirri (Tuffrau 1979). Our classification was accepted by the founder of the Kahliellidae (Tuffrau 1987, Tuffrau & Fleury 1994) and some other workers, for example, Foissner & Foissner (1988, p. 82), Eigner (1995), Lynn & Small (2002), Jankowski (2007), Lynn (2008) and is retained in the present review (see also Berger 2007a). Eigner (1997; see also Eigner 1999, p. 46) established the Parakahliellidae comprising a variety of genera, for example, *Onychodromus quadricornutus* (now in *Styxophrya* Foissner et al., 2004) and most other stylonychines, some flexible oxy-

trichids (dorsal kinety fragmentation present), and *Urosomoida agiliformis*, a non-oxytrichid Dorsomarginalia according to a more recent hypothesis (Berger 2008). Both detailed classical analyses as well as molecular studies strongly indicate that Eigner's (1997, 1999) classification is artificial. Further details, see below.

Berger & Foissner (1989b) assigned a third species (*Parakahliella haideri*) to the present genus because its ventral cirral pattern resembles that of *P. macrostoma* and *P. terricola*, and in particular because of the unique mode of dorsal morphogenesis, especially the conservation of parental kineties 4 and 5 as new kinety 4 in the postdividers. This is indeed a rather good feature suggesting that these three species form a monophyletic group. Thus, Berger & Foissner (1989b) removed the feature "increased number of left marginal rows and preservation of some parts of the parental left marginal infraciliature" from the diagnosis provided by Berger et al. (1985), a characteristic which would exclude *P. haideri* from the present genus.

Shi et al. (1999, p. 99) and Shi (1999, p. 251, 252) synonymised *Parakahliella* with *Kahliella*. However, these two genera differ, inter alia, in the dorsal morphogenesis (parental kineties retained vs. not), arrangement of caudal cirri (usually each two or more cirri on kineties 1 and 2 vs. many cirri on kinety 1), and the adoral zone (ordinary against similar as in *Gonostomum*). Consequently, the synonymy of *Parakahliella* and *Kahliella* is not justified.

In *Parakahliella macrostoma*, *P. terricola*, *P. haideri*, and *P. binucleata* the undulating membranes are usually distinctly curved and optically intersecting. Thus, we supposed that the two further species classified in *Parakahliella*, namely *P. namibicola* and *P. halophila*, might belong to a new subgenus or genus (Foissner et al. 2002a). In the present review I transfer the three African species to *Afrokahliella* because they lack the preservation of parental dorsal kineties 4 and 5 characterising *Parakahliella* very well (Berger & Foissner 1989). Their continuance in *Parakahliella* would make the characterisation of this genus very non-specific. For some biogeographical comments, see *Afrokahliella*.

The general cirral pattern of *Fragmocirrus* Foissner, 2000 is very similar to that of *Parakahliella*, indicating a close relationship. They differ in the transverse cirri (present vs. lacking) and the preservation of parental dorsal kineties (lacking vs. present).

Parentocirrus Voß, 1997 also has a similar ventral cirral pattern. However, it has a dorsal kinety fragmentation in kinety 3, strongly indicating (actually proving) that it belongs to the oxytrichids (for review, see Berger 1999, p. 880; 2008, p. 539). By contrast, the lack of such a fragmentation in *Parakahliella* suggests that it is a non-oxytrichid Dorsomarginalia (Berger 2008).

Bistichella Berger, 2008 lacks a dorsomarginal kinety indicating that the similarity in the cirral pattern is mainly based on convergent evolution (for review, see Berger 2008, p. 532).

According to Eigner (1995, p. 364), *Coniculostomum* Njine, 1979 is a close relative of *Parakahliella* and some other "kahliellid" genera. However, *Coniculostomum* has a dorsal kinety fragmentation and a rigid body proving that it is a stylonychine oxytrichid. Very likely it is the sistergroup of *Stylonychia* (Berger 1999, p. 76, 606).

Table 23 Morphometric data on *Afrokahliella binucleata* (bin, from Foissner et al. 2002a), *Afrokahliella halophila* [k] (ha1, type population from USA two days after rewetting the sample [= population I in Foissner et al. 2002a]; ha2, type population from USA six days after rewetting the sample [= population II in Foissner et al. 2002a]; ha3, Namibian site [59] population [= population III in Foissner et al. 2002a]; ha4, Namibian site (18) population [= population IV in Foissner et al. 2002a]; ha5, populations ha1–ha4 pooled [= populations V in Foissner et al. 2002a]; all data from Foissner et al. 2002a), *Afrokahliella namibicola* (nam, from Foissner et al. 2002a), *Parakahliella haideri* (hai, from Berger & Foissner 1989b), *Parakahliella macrostoma* (ma1, from Foissner 1982; ma2, from Berger et al. 1985), and *Parakahliella terricola* (ter, from Buitkamp 1977)

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	bin	132.8	128.0	19.3	3.6	14.5	106.0	173.0	29
	hai	127.1	125.5	12.5	2.0	9.8	105.0	160.0	40
	ha1	87.6	88.0	9.2	2.2	10.5	72.0	104.0	17
	ha2	94.9	89.0	16.5	4.0	17.4	76.0	136.0	17
	ha3	84.9	87.0	10.1	2.9	11.8	67.0	108.0	21
	ha4	77.1	78.0	7.8	1.9	10.1	61.0	88.0	17
	ha5	86.0	85.0	12.7	1.5	14.8	61.0	136.0	72
	ma1	106.4	103.5	12.6	3.4	11.8	86.0	130.0	10
	ma2	127.4	–	20.1	–	15.8	98.0	171.0	25
	nam	80.8	82.0	10.7	2.2	13.2	57.0	105.0	23
Body, width	bin	59.8	57.0	14.0	2.6	23.4	36.0	100.0	29
	hai	52.5	51.5	8.4	1.3	15.9	35.0	73.0	40
	ha1	36.3	37.0	4.1	1.0	11.3	29.0	44.0	17
	ha2	49.5	50.0	9.5	2.3	19.1	34.0	75.0	17
	ha3	32.8	32.0	4.1	0.9	12.4	27.0	42.0	21
	ha4	37.5	37.0	3.9	1.0	10.5	30.0	44.0	17
	ha5	38.7	37.0	8.5	1.0	22.0	27.0	75.0	72
	ma1	40.3	39.0	6.7	2.1	16.6	28.0	53.0	10
	ma2	38.4	–	8.9	–	23.1	27.0	61.0	25
	nam	30.8	30.0	5.2	1.1	16.8	20.0	45.0	23
Body length:width, ratio	nam	2.7	2.5	0.5	0.1	17.1	1.8	3.9	23
Adoral zone of membranelles, length	bin	41.5	38.0	9.8	1.8	23.7	29.9	64.0	29
	hai	48.3	48.0	6.6	1.1	13.8	33.0	60.0	40
	ha1	23.9	24.0	2.0	0.5	8.4	19.0	27.0	17
	ha2	30.8	27.0	8.9	2.2	28.8	22.0	57.0	17
	ha3	30.7	31.0	4.6	1.0	15.1	22.0	40.0	21
	ha4	19.2	19.0	2.2	0.5	11.6	14.0	23.0	17
	ha5	26.4	25.0	7.1	0.8	26.8	14.0	57.0	72
	ma1	40.7	40.0	6.2	2.0	15.3	27.0	50.0	10
	ma2	44.5	–	11.3	–	25.2	32.0	76.0	21
	nam	21.8	22.0	1.8	0.4	8.4	18.0	26.0	23
Length of adoral zone:body length, ratio (in %)	bin	31.1	31.0	4.2	0.8	13.6	21.0	40.0	29
Body length:length of adoral zone, ratio	nam	3.7	3.6	0.4	0.1	11.9	3.0	4.8	23
Adoral membranelles, number	bin	38.7	37.0	8.5	1.6	22.0	27.0	57.0	29
	hai	47.7	47.0	6.8	1.1	14.2	34.0	62.0	37
	ha1	22.4	22.0	1.8	0.5	8.2	18.0	25.0	17
	ha2	29.3	27.0	7.1	1.7	24.3	22.0	48.0	17
	ha3	33.5	34.0	4.2	0.9	12.5	25.0	44.0	21
	ha4	20.8	21.0	1.7	0.4	8.3	17.0	24.0	17
	ha5	26.9	24.0	6.8	0.8	25.2	17.0	48.0	72

Table 23 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Adoral membranelles, number	ma1	52.5	53.5	5.9	1.9	11.2	38.0	61.0	10
	ma2	50.8	–	12.6	–	24.8	40.0	75.0	8
	nam	24.7	24.0	2.2	0.5	9.0	21.0	31.0	23
	ter	28.0	–	–	–	–	–	–	?
Anterior body end to anterior macronuclear nodule, distance	nam	23.8	24.0	3.4	0.7	14.1	17.0	32.0	23
Anterior macronuclear nodule, length	bin	19.8	19.0	3.7	0.7	18.8	15.0	30.0	29
	nam	14.5	15.0	3.1	0.6	21.1	9.0	21.0	23
Anterior macronuclear nodule, width	bin	8.2	8.0	1.1	0.2	13.2	7.0	11.0	29
	nam	8.0	8.0	1.1	0.2	13.4	6.0	10.0	23
Posterior macronuclear nodule, length	hai	11.6	10.0	4.6	0.8	39.5	7.0	25.0	40
	ha1	14.8	15.0	3.2	0.8	21.5	10.0	22.0	17
	ha2	12.6	12.0	4.1	1.0	32.9	7.0	20.0	17
	ha3	11.3	12.0	2.8	0.6	24.9	6.0	15.0	21
	ha4	13.5	13.0	2.4	0.6	17.6	10.0	18.0	17
	ha5	12.9	13.0	3.4	0.4	26.1	6.0	22.0	72
	ma1 [m]	9.3	9.3	1.5	0.5	15.7	6.6	12.0	10
	ma2	13.1	–	2.7	–	20.7	8.0	19.0	25
Posterior macronuclear nodule, width	hai	8.2	8.0	1.4	0.2	17.3	6.0	12.0	40
	ha1	8.9	9.0	1.3	0.3	14.3	7.0	11.0	17
	ha2	6.8	7.0	1.7	0.4	25.4	4.0	10.0	17
	ha3	6.4	6.0	0.9	0.2	13.5	5.0	8.0	21
	ha4	10.8	10.0	1.8	0.4	16.7	8.0	15.0	17
	ha5	8.1	8.0	2.3	0.3	27.9	4.0	15.0	72
	ma1 [m]	5.4	5.3	1.5	0.5	28.0	4.0	8.0	10
	ma2	8.3	–	1.6	–	19.5	6.0	12.0	25
Macronuclear nodules, distance in between	nam	5.8	7.0	3.6	0.8	61.8	0.0	12.0	23
Macronuclear figure, length	nam	34.4	35.0	7.3	1.5	21.3	21.0	48.0	23
Macronuclear nodules, number	bin	2.0	2.0	0.0	0.0	0.0	2.0	2.0	29
	hai	6.2	6.0	0.6	0.1	10.5	5.0	9.0	40
	ha1	4.1	4.0	0.5	0.1	11.8	4.0	6.0	17
	ha2	5.9	5.0	1.6	0.4	26.3	4.0	8.0	17
	ha3	4.8	4.0	1.2	0.3	24.8	3.0	8.0	21
	ha4	3.8	4.0	0.6	0.1	14.9	2.0	4.0	17
	ha5	4.7	4.0	1.3	0.2	28.2	2.0	8.0	72
	ma1	10.6	10.5	1.4	0.5	13.5	8.0	13.0	10
	ma2	7.4	–	1.4	–	18.7	5.0	10.0	25
	nam	2.1	2.0	0.4	0.1	19.6	1.0	4.0	113
	ter	8.0	–	–	–	–	–	–	?
Anterior micronucleus, length	bin	3.0	3.0	–	–	–	3.0	4.0	29
Anterior micronucleus, width	bin	2.6	2.5	0.4	0.1	14.1	2.0	4.0	29
Micronuclei, number	bin	3.2	3.0	1.3	0.2	40.3	1.0	7.0	29
	hai	4.0	4.0	1.3	0.2	31.9	2.0	7.0	40
	ha1	2.7	3.0	0.7	0.2	26.5	2.0	4.0	17
	ha2	2.8	2.0	1.2	0.3	43.4	1.0	5.0	17
	ha3	4.1	4.0	1.0	0.2	25.5	2.0	6.0	21
	ha4	2.5	2.0	0.9	0.2	34.6	2.0	4.0	17
	ha5	3.1	3.0	1.2	0.1	38.0	1.0	6.0	72
	ter	4.0	–	–	–	–	–	–	?

Table 23 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Posterior micronucleus, diameter	hai	2.6	3.0	0.5	0.8	19.4	2.0	3.0	40
	ha1	2.2	2.0	–	–	–	2.0	3.0	17
	ha2	2.3	3.0	–	–	–	2.0	3.0	17
	ha3	2.1	2.0	–	–	–	2.0	3.0	21
	ha4	2.1	2.0	–	–	–	2.0	3.0	17
	ha5	2.2	2.0	–	–	–	2.0	3.0	72
Anterior body end to paroral, distance	nam	4.7	5.0	0.8	0.2	17.9	3.0	6.0	23
Paroral, length	nam	9.1	9.0	1.7	0.4	18.2	7.0	14.0	23
Anterior body end to endoral, distance	nam	5.1	5.0	0.9	0.2	16.9	4.0	6.0	23
Endoral, length	nam	12.4	12.0	2.0	0.4	15.9	9.0	18.0	23
Anterior body end to buccal cirrus, distance	nam	4.9	5.0	0.8	0.2	16.7	3.0	6.0	23
Anterior body end to end of parabuccal cirral row, distance	nam	17.8	20.0	4.6	1.0	26.0	11.0	26.0	23
Anterior body end to end of left frontoventral row, distance	nam	55.3	57.0	9.1	1.9	16.5	38.0	69.0	23
Anterior body end to end of right frontoventral row, distance	nam	50.8	51.0	8.3	1.7	16.3	35.0	69.0	23
Anterior body end to right marginal row, distance	nam	6.8	6.0	2.3	0.5	33.5	4.0	12.0	23
Posterior body end to right marginal row, distance	nam	3.1	3.0	1.5	0.3	49.7	1.0	7.0	23
Posterior body end to left marginal row, distance	nam	3.4	3.0	1.9	0.4	54.0	1.0	9.0	23
Enlarged frontal cirri, number	bin	3.0	3.0	0.0	0.0	0.0	3.0	3.0	29
	hai	3.0	3.0	0.4	0.1	13.2	2.0	5.0	39
	ha1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	ha2	3.1	3.0	–	–	–	3.0	4.0	17
	ha3	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	ha4	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	ha5	3.0	3.0	–	–	–	3.0	4.0	72
	ma1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	ma2	3.0	–	0.0	–	0.0	3.0	3.0	25
	nam	3.0	3.0	0.0	0.0	0.0	3.0	3.0	23
	ter	3.0	–	–	–	–	–	–	?
Buccal cirral row, number of cirri	bin	1.5	1.0	0.6	0.1	37.9	1.0	3.0	29
	hai	3.0	3.0	0.7	0.1	22.2	1.0	4.0	40
	ha1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
	ha2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
	ha3	1.1	1.0	–	–	–	1.0	2.0	21
	ha4	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
	ha5	1.0	1.0	–	–	–	1.0	2.0	72
	ma1	3.9	3.5	1.0	0.3	26.8	3.0	6.0	10
	ma2	3.0	–	0.8	–	27.7	2.0	5.0	25
	nam	1.2	1.0	–	–	–	0.0	2.0	23
Cirri left of parabuccal row, number	nam	0.7	0.0	0	–	–	0.0	3.0	23
Cirri (= parabuccal cirri) behind right frontal cirrus, number	bin	3.1	3.0	0.4	0.1	13.0	2.0	4.0	25
	hai	2.2	2.0	0.4	0.1	19.8	1.0	3.0	40
	ha1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
	ha2	2.1	2.0	–	–	–	2.0	3.0	17

Table 23 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Cirri (= parabuccal cirri) behind right frontal cirrus, number	ha3	2.5	2.0	0.8	0.2	32.2	1.0	4.0	21
	ha4	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
	ha5	2.2	2.0	0.5	0.1	23.5	1.0	4.0	72
	ma1 [d]	4.3	–	0.7	–	16.3	3.0	5.0	9
	ma2 [d]	4.5	–	1.2	–	26.6	3.0	8.0	15
	nam	3.9	4.0	1.5	0.3	37.7	2.0	8.0	23
Frontoventral rows, number	bin [g]	5.4	5.0	1.7	0.4	31.5	3.0	9.0	19
	nam [i]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	23
Cirral rows right of median, number [n]	ma1	4.1	4.0	0.3	0.1	7.3	4.0	5.0	10
	ma2	4.4	–	0.9	–	19.7	4.0	8.0	25
Left frontoventral row, number of cirri	hai	13.6	13.0	3.4	0.6	25.2	4.0	20.0	37
	ha1	5.8	6.0	1.6	0.4	27.3	2.0	8.0	17
	ha2	8.2	9.0	2.2	0.5	26.4	5.0	13.0	17
	ha3	8.0	7.0	2.2	0.5	27.7	5.0	12.0	21
	ha4	4.0	4.0	2.1	0.5	51.5	1.0	11.0	17
	ha5	6.6	6.0	2.6	0.3	39.8	1.0	13.0	72
	ma1 [o]	24.7	24.0	5.2	1.6	20.0	14.0	35.0	10
	ma2	17.3	–	3.2	–	18.8	13.0	24.0	15
	nam	20.2	20.0	2.9	0.6	14.5	15.0	25.0	23
Right frontoventral row, number of cirri	hai	16.3	16.0	2.7	0.4	16.5	10.0	22.0	37
	ha1 [l]	5.4	5.0	1.0	0.2	18.6	4.0	7.0	17
	ha2 [l]	7.1	7.0	1.7	0.4	23.8	5.0	12.0	17
	ha3 [l]	7.3	7.0	1.5	0.3	20.0	5.0	11.0	21
	ha4 [l]	4.1	4.0	0.6	0.1	13.7	3.0	5.0	17
	ha5 [l]	6.0	6.0	1.8	0.2	30.2	3.0	12.0	72
	ma1	24.8	24.0	4.0	1.3	16.3	18.0	33.0	10
	ma2	17.4	–	3.5	–	19.9	13.0	27.0	22
	nam	20.0	20.0	2.5	0.5	12.5	15.0	24.0	23
Left marginal rows, number	bin [h]	2.0	2.0	1.0	0.2	51.9	1.0	6.0	27
	ma1	4.2	4.0	0.4	0.1	9.5	4.0	5.0	10
	ma2	2.9	–	0.8	–	26.7	2.0	5.0	25
	nam	1.1	1.0	–	–	–	1.0	2.0	23
Left marginal row (= inner left marginal row, = left marginal row 1), number of cirri	bin [f]	37.4	36.0	8.2	1.5	21.9	20.0	54.0	29
	hai	32.3	32.0	3.9	0.6	12.0	23.0	40.0	40
	ha1	26.9	28.0	2.6	0.6	9.7	22.0	31.0	17
	ha2	30.6	31.0	3.8	0.9	12.4	23.0	37.0	17
	ha3	32.1	32.0	4.1	0.9	12.9	23.0	39.0	21
	ha4	26.2	26.0	2.7	0.7	10.4	21.0	33.0	17
	ha5	29.1	29.0	4.2	0.5	14.4	21.0	39.0	72
	ma1 [f]	29.6	30.0	5.1	1.7	17.1	19.0	35.0	9
	ma2 [f]	25.0	–	6.8	–	27.1	14.0	47.0	24
	nam	26.4	26.0	3.5	0.7	13.4	21.0	33.0	23
	ter [f]	23.0	–	–	–	–	–	–	?
Left marginal row 2, number of cirri [e]	ma1	20.7	21.0	5.4	1.8	26.1	13.0	29.0	9
	ma2	16.5	–	4.3	–	25.7	10.0	27.0	25
Left marginal row 3, number of cirri [e]	ma1	15.4	16.0	3.5	1.2	22.7	7.0	20.0	8
	ma2	8.7	–	5.6	–	63.8	3.0	29.0	23
Left marginal row 4, number of cirri [e]	ma1	5.9	4.5	3.2	1.1	53.9	3.0	13.0	8
	ma2	6.7	–	1.5	–	22.2	5.0	8.0	4
Outer right marginal row, number of cirri	bin	43.0	43.0	6.3	1.2	14.6	31.0	57.0	27

Table 23 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Outer right marginal row, number of cirri	hai	32.6	33.0	4.0	0.7	12.4	25.0	43.0	38
	ha1	33.7	35.0	3.0	0.7	8.8	29.0	39.0	17
	ha2	37.2	36.0	6.6	1.6	17.9	26.0	50.0	17
	ha3	38.2	39.0	4.3	0.9	11.3	27.0	45.0	21
	ha4	31.0	30.0	3.1	0.8	9.9	27.0	40.0	17
	ha5	35.2	35.0	5.3	0.6	15.0	26.0	50.0	72
	ma1	33.6	34.0	4.2	1.3	12.6	25.0	40.0	10
	ma2	29.2	–	7.1	–	24.4	13.0	37.0	24
	nam [j]	30.5	30.0	3.4	0.7	11.0	24.0	38.0	23
	ter	24.0	–	–	–	–	–	–	?
Inner right marginal row, number of cirri	hai	9.3	8.0	4.7	0.8	50.9	2.0	18.0	35
	ha1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	ha2	4.1	0.0	–	–	–	0.0	22.0	17
	ha3	3.0	2.0	3.1	0.7	102.0	0.0	10.0	21
	ha4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	ha5	1.9	0.0	–	–	–	0.0	22.0	72
	ma1	22.8	21.0	5.0	1.6	21.8	18.0	35.0	10
	ma2	16.3	–	4.2	–	25.7	8.0	25.0	25
Additional cirral rows, number	hai [b]	1.1	1.0	0.8	0.1	77.3	0.0	3.0	33
	ha1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	ha2	0.5	0.0	–	–	–	0.0	1.0	17
	ha3	0.6	1.0	–	–	–	0.0	2.0	21
	ha4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	ha5	0.3	0.0	–	–	–	0.0	2.0	72
Dorsal kineties, number	bin	4.1	4.0	–	–	–	4.0	5.0	13
	hai [c]	5.0	5.0	0.0	0.0	0.0	5.0	5.0	24
	ha1	4.1	4.0	–	–	–	4.0	5.0	17
	ha2	4.1	4.0	–	–	–	4.0	5.0	17
	ha3	4.3	4.0	–	–	–	4.0	5.0	21
	ha4	4.0	4.0	0.0	0.0	0.0	4.0	4.0	17
	ha5	4.1	4.0	–	–	–	4.0	5.0	72
	ma1	5.0	5.0	0.0	0.0	0.0	5.0	5.0	10
	ma2	5.0	–	0.0	–	0.0	5.0	5.0	25
	nam	4.0	4.0	0.0	0.0	0.0	4.0	4.0	23
	ter	5.0	–	–	–	–	–	–	?
Dorsal kinety 1, number of basal body pairs	hai	28.5	28.0	3.5	0.7	12.4	21.0	34.0	29
	ha1	11.7	12.0	1.8	0.4	15.2	9.0	17.0	17
	ha2	17.3	16.0	5.1	1.2	29.5	12.0	32.0	17
	ha3	14.7	15.0	1.7	0.4	11.4	12.0	18.0	21
	ha4	9.5	9.0	1.2	0.3	12.4	8.0	12.0	17
	ha5	13.4	13.0	4.0	0.5	30.0	8.0	32.0	72
Dorsal kinety 2, number of basal body pairs	hai	29.7	30.0	3.6	0.7	12.3	22.0	38.0	25
	ha1	15.1	15.0	1.4	0.3	9.3	13.0	17.0	17
	ha2	20.6	20.0	5.3	1.3	25.9	11.0	31.0	17
	ha3	16.3	16.0	2.4	0.5	14.4	13.0	20.0	21
	ha4	11.9	12.0	1.4	0.3	11.7	10.0	15.0	17
	ha5	16.0	15.0	4.3	0.5	26.5	10.0	31.0	72
Dorsal kinety 3, number of basal body pairs	hai	26.4	27.0	3.4	0.7	12.7	19.0	33.0	24
	ha1	12.7	13.0	1.3	0.3	9.9	11.0	15.0	17
	ha2	17.4	417.0	4.1	1.0	23.8	12.0	29.0	17

Table 23 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Dorsal kinety 3, number of basal body pairs	ha3	15.2	15.0	3.0	0.7	19.5	11.0	23.0	21
	ha4	9.9	9.0	1.4	0.3	13.8	8.0	13.0	17
	ha5	13.9	14.0	3.9	0.5	27.7	8.0	29.0	72
Dorsal kinety 4, number of basal body pairs	hai [d]	8.2	8.0	1.9	0.4	22.7	4.0	11.0	18
	ha1	0.1	0.0	–	–	–	0.0	0.0	17
	ha2	0.6	0.0	–	–	–	0.0	7.0	17
	ha3	1.1	0.0	–	–	–	0.0	9.0	21
	ha4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	ha5	0.9	0.0	–	–	–	0.0	9.0	72
	ma2 [d]	10.6	–	2.0	–	18.6	7.0	13.0	12
Dorsal kinety 5, number of basal body pairs	hai [e]	12.1	12.0	1.9	0.4	15.4	9.0	16.0	27
	ha1	5.5	6.0	1.2	0.3	22.5	3.0	8.0	17
	ha2	8.5	8.0	2.4	0.6	28.0	5.0	15.0	17
	ha3	8.6	9.0	2.1	0.4	23.8	5.0	12.0	21
	ha4	4.8	5.0	0.8	0.2	17.5	3.0	6.0	17
	ha5	6.9	6.0	2.4	0.3	35.2	3.0	15.0	72
	ma2 [e]	14.5	–	2.4	–	16.7	11.0	19.0	12
Caudal cirri, total number	ma1	5.0	5.0	0.9	0.3	17.9	4.0	6.0	10
	ma2	4.8	–	0.8	–	16.5	3.0	7.0	25
	nam	4.8	5.0	1.6	0.3	32.4	3.0	9.0	23
	ter	3.0	–	–	–	–	–	–	?
Caudal cirri on dorsal kinety 1, number	bin	5.1	4.0	2.3	0.5	44.9	2.0	12.0	25
	hai	2.7	3.0	0.5	0.1	19.7	2.0	4.0	35
	ha1	2.1	2.0	0.4	0.1	20.8	1.0	3.0	17
	ha2	2.1	2.0	0.9	0.2	40.5	1.0	4.0	17
	ha3	2.7	3.0	0.7	0.1	24.7	1.0	4.0	21
	ha4	1.9	2.0	–	–	–	1.0	2.0	17
	ha5	2.2	2.0	0.7	0.1	29.5	1.0	4.0	72
	ma2	3.0	–	0.6	–	18.6	2.0	5.0	25
	nam	3.1	3.0	1.2	0.3	37.7	1.0	6.0	23
Caudal cirri on dorsal kinety 2, number	bin	3.2	3.0	1.4	0.3	44.9	1.0	7.0	20
	hai	1.1	1.0	0.3	0.1	29.3	1.0	2.0	34
	ha1	1.2	1.0	–	–	–	1.0	2.0	17
	ha2	1.1	1.0	–	–	–	1.0	2.0	17
	ha3	1.4	1.0	–	–	–	1.0	3.0	21
	ha4	1.1	1.0	–	–	–	1.0	2.0	17
	ha5	1.2	1.0	–	–	–	1.0	3.0	72
	ma2	1.7	–	0.4	–	24.8	1.0	2.0	25
	nam	1.4	1.0	0.6	0.1	41.1	1.0	3.0	23
Caudal cirri on dorsal kinety 3, number	bin	1.9	2.0	0.5	0.1	26.5	1.0	3.0	20
	nam	0.3	0.0	–	–	–	0.0	2.0	23

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean. ? = sample size not indicated (if only one value is known, it is listed in the mean column; if two values are available, then they are listed as Min and Max). Data based on protargol-impregnated specimens.

[b] Single cirri and rows with only two or three cirri not included.

[c] Parental row (kinety 4) between kinety 3 and kinety 5 included.

Table 23 Continued

[d] Right frontal cirrus included. Values for type population from Berger et al. (1985).

[e] Numbering is from inside to outside, that is, left marginal row 2 is left of the inner row (= left marginal row 1).

[f] This is the inner row (= left marginal row 1).

[g] Cirri (parabuccal row) behind right frontal cirrus not included.

[h] Short fragments included.

[i] Anlagen I and II not included.

[j] *Afrokahliella namibicola* has invariably only one right marginal row.

[k] All populations in exponential growth phase as evident from many dividers contained in the slides.

[l] Includes all postoral cirri that do not belong to the marginal cirral rows.

[m] Nodule (anterior, posterior, ...) not indicated.

[n] Foissner (1982) did not distinguish between frontoventral rows and right marginal rows.

[o] Parabuccal cirri likely included.

Species included in *Parakahliella* (alphabetically arranged basionyms are given): (1) *Parakahliella haideri* Berger & Foissner, 1989; (2) *Paraurostyla macrostoma* Foissner, 1982 (type); (3) *Paraurostyla terricola* Buitkamp, 1977.

Species misplaced in *Parakahliella*: The following species have been previously assigned to *Parakahliella* because of the very similar ventral cirral pattern. However, they lack the preservation of parental dorsal kineties and therefore they have been classified in a new genus.

Parakahliella binucleata Foissner, Agatha & Berger, 2002a. Remarks: Now *Afrokahliella binucleata* (p. 449).

Parakahliella halophila Foissner, Agatha & Berger, 2002a. Remarks: Now *Afrokahliella halophila* (p. 440).

Parakahliella namibicola Foissner, Agatha & Berger, 2002a. Remarks: Now type of *Afrokahliella* (p. 434).

Key to *Parakahliella* species

If you cannot identify your specimen/population with the key below, see also *Afrokahliella* (four dorsal kineties; p. 432), *Fragmocirrus* (indistinct transverse cirri present; p. 455), *Bistichella* (only three bipolar dorsal kineties, that is, dorsomarginal kinety lacking; Berger 2008, p. 532), or *Parentocirrus* (with oxytrichid dorsal kinety fragmentation; Berger 1999, p. 878).

1 More than one distinct left marginal row (Fig. 73a, d, f, 74a). **2**

- Usually only one distinct left marginal row (Fig. 75a, d). . . . . *Parakahliella haideri* (p. 422)

2 On average 53 (range 38–75) adoral membranelles (Fig. 73d, f). . . . . *Parakahliella macrostoma* (p. 407)
- About 28 adoral membranelles (Fig. 74a). . . . . *Parakahliella terricola* (p. 418)

Parakahliella macrostoma (Foissner, 1982) Berger, Foissner & Adam, 1985
(Fig. 73a–q, Table 23)

1982 ***Paraurostyla macrostoma* nov. spec.**[1] – Foissner, Arch. Protistenk., 126: 43, Abb. 5a–e, Tabelle 8 (Fig. 73a–e; original description; the holotype slide [accession number 1981/83] is deposited in the Oberösterreichische Landesmuseum in Linz, Upper Austria; Aescht 2008, p. 163).

1985 ***Parakahliella macrostoma* (Foissner, 1982) nov. comb.** – Berger, Foissner & Adam, Protistologica, 21: 297, 309, Fig. 1–12, Table 1, 4 (Fig. 73f–q; combination with *Parakahliella* and cell division).

1995 ***Parakahliella macrostoma* (Foissner, 1982) Berger, Foissner and Adam, 1985** – Eigner, Europ. J. Protistol., 31: 355, Fig. 41 (Fig. 73f; redefinition of the Kahliellidae).

1997 ***Parakahliella macrostoma* (Foissner, 1982) Berger, Foissner & Adam, 1985** – Eigner, J. Euk. Microbiol., 44: 563, Fig. 24 (Fig. 73f; diagrammatic representation of cirral pattern and ontogenesis).

2001 ***Parakahliella macrostoma* (Foissner, 1982) Berger, Foissner and Adam, 1985** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 70 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).

2008 ***Parakahliella*** – Lynn, Ciliated protozoa, p. 164, Fig. 7.7Ca–d (Fig. 73f, h, k, m; revision of ciliates).

Nomenclature: No derivation of the species-group name is given in the original description. The name *macrostom·us, -a, um* (m; f; n; big-mouthed) is a composite of the Greek adjective *makros* (large) and the Greek noun *to stóma* (mouth) and obviously refers to the large oral apparatus. Type species of *Parakahliella*.

Remarks: For a comparison with *P. terricola* see there. Foissner et al. (1987a, p. 158) compared *P. macrostoma* with *Onychodromus quadricornutus* Foissner, Schlegel & Prescott, 1987 (now *Styxophrya quadricornuta*; Foissner et al. 2004*)* because of a similar general appearance. However, they can be easily distinguished, inter alia, by the habitat (terrestrial vs. limnetic), the consistence of the cell (flexible vs. rigid), and the dorsal morphogenesis (kinety fragmentation lacking vs. present).

Eigner (1999, p. 46), who made a phylogenetic analysis based on six characters, found a close relationship of *P. macrostoma* with *Neogeneia hortualis*, *Onychodromus quadricornutus*, *Kerona polyporum*, *Paraurostyla weissei*, *Parentocirrus hortualis*, and a group with flexible and rigid oxytrichids. This tree contradicts all other morphological trees and basically all molecular phylogenies, which, for example, summarise all rigid oxytrichids in the stylonychines.

[1] Foissner (1982) provided the following diagnosis: In vivo etwa 170–220 × 50–70 µm große *Paraurostyla* mit durchschnittlich 52 adoralen Membranellen und je 4–5 Cirrenreihen links und rechts der Medianen. 4–6 Caudalcirren. Dicht unter der Pellicula netzartig angeordnete, etwa 1–2 µm große, gelb gefärbte, zylindroide Kristalle.

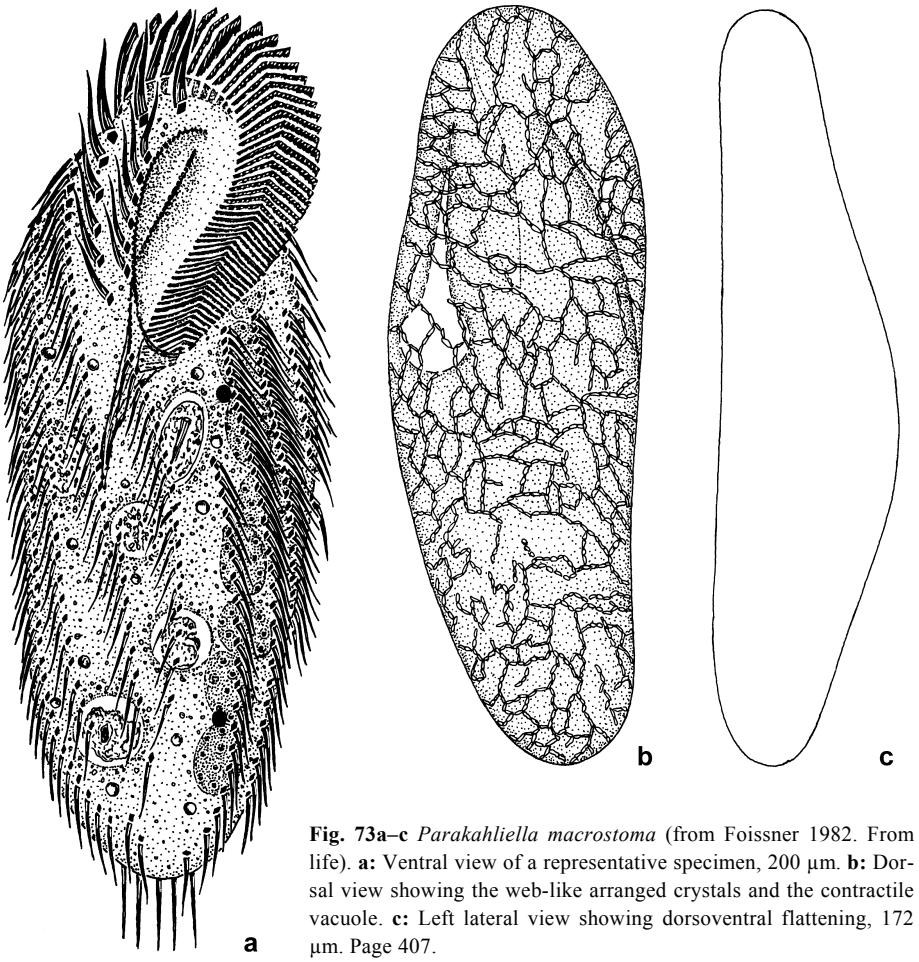


Fig. 73a–c *Parakahliella macrostoma* (from Foissner 1982. From life). **a:** Ventral view of a representative specimen, 200 µm. **b:** Dorsal view showing the web-like arranged crystals and the contractile vacuole. **c:** Left lateral view showing dorsoventral flattening, 172 µm. Page 407.

Morphology: At first the type population from the Lower Austrian lowland is described (Foissner 1982; Fig. 73a–e), followed by additional and deviating data from the alpine population studied by Berger et al. (1985; Fig. 73f, g).

Specimens of type population in life 170–220 × 50–70 µm. Body shape moderately variable, usually slightly S-shaped, rarely more or less oblong; posterior portion slightly to distinctly narrowed; right margin slightly concave, left one invariably distinctly convex at level of contractile vacuole; dorsal side usually vaulted in middle area of leftmost dorsal kineties (Fig. 73a, b). Body flexible, about 2:1 flattened dorsoventrally (Fig. 73c). 8–13, on average 10.5 macronuclear nodules left of median in middle cell portion; individual nodules about 20 × 12 µm, with many small chromatin bodies; in one live specimen two micronuclei (4 µm across) observed. Contractile vacuole slightly ahead of mid-body near left cell margin; one anterior collecting canal, occasionally with a vesicle at level of adoral zone. Pellicle colour-

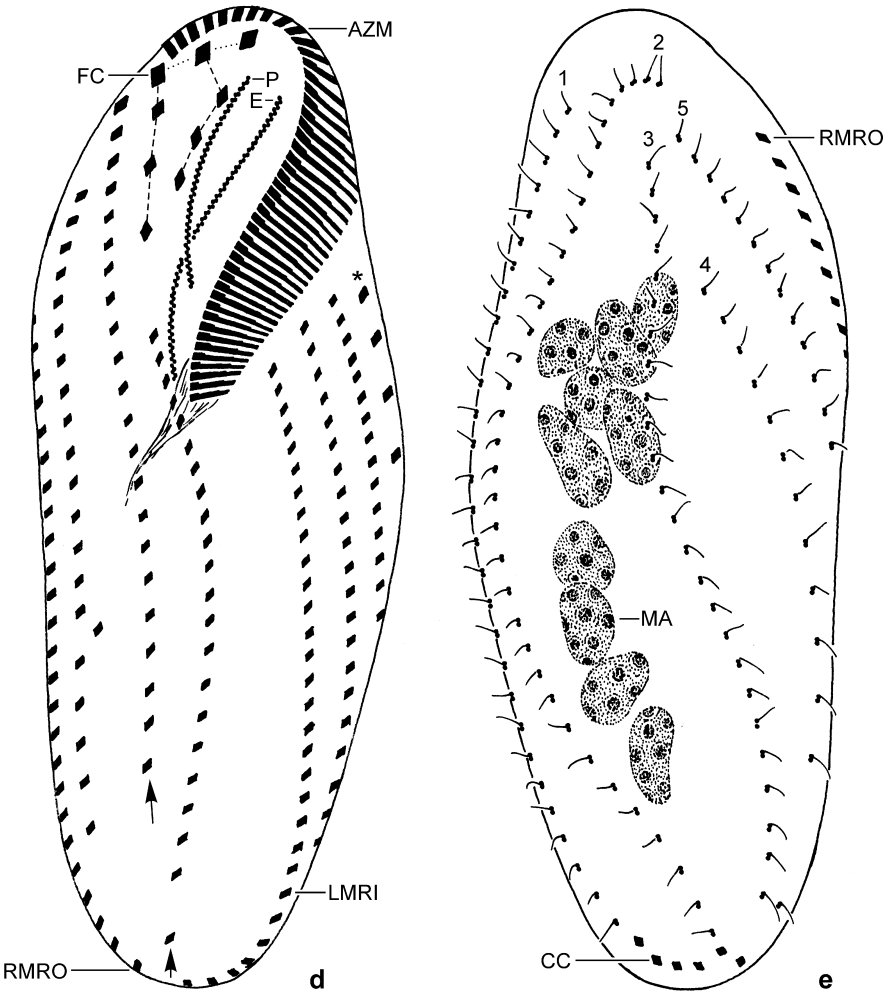


Fig. 73d, e *Parakahliella macrostoma* (from Foissner 1982. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus, 97 µm. Frontal cirri connected by dotted line, cirri originating from anlage II, respectively, III connected by broken line. Short arrow denotes rear end of left frontoventral row, long arrow marks right frontoventral row. AZM = adoral zone of membranelles, E = endoral, FC = right frontal cirrus, LMRI = inner left marginal row (= left marginal row 1), P = paroral, RMRO outer right marginal row, 1–5 = dorsal kineties (kinety 4 is a parental row, kinety 5 is a dorsomarginal kinety). Page 407.

less; at low magnification, specimens slightly brownish due to the many, web-like arranged subpellicular crystals; individual crystals 1–2 µm long, yellowish, cylindrical. Cortical granules lacking. Cytoplasm with moderately many, 1–3 µm-sized, slightly yellowish, shining globules, and 10–20 µm-sized food vacuoles mainly in middle body portion. Movement slow, adheres close to soil particles.

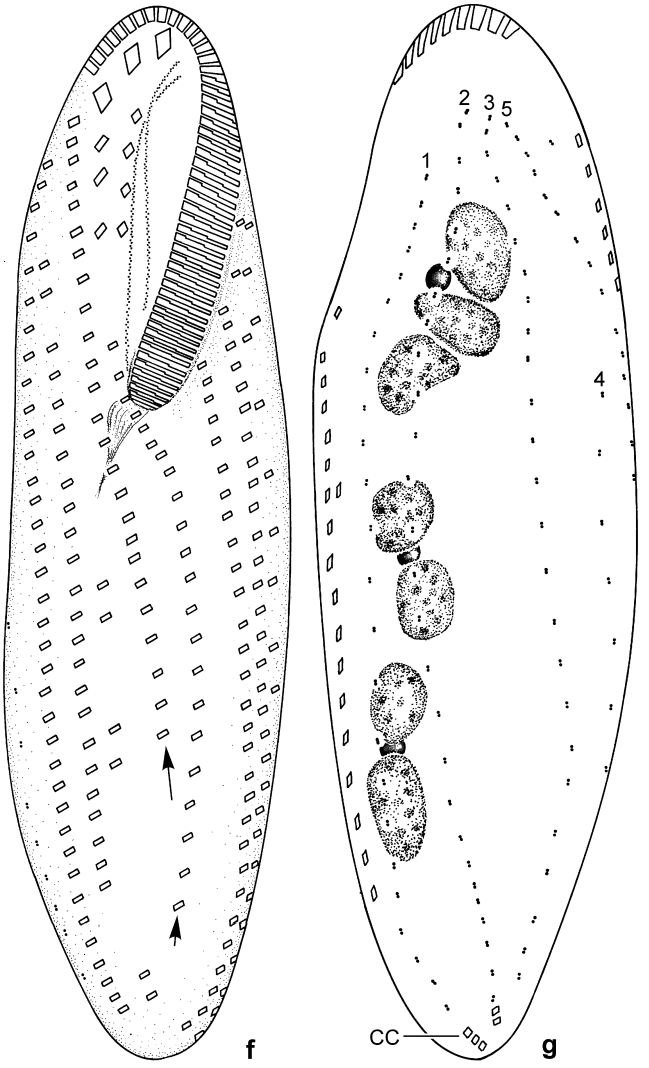
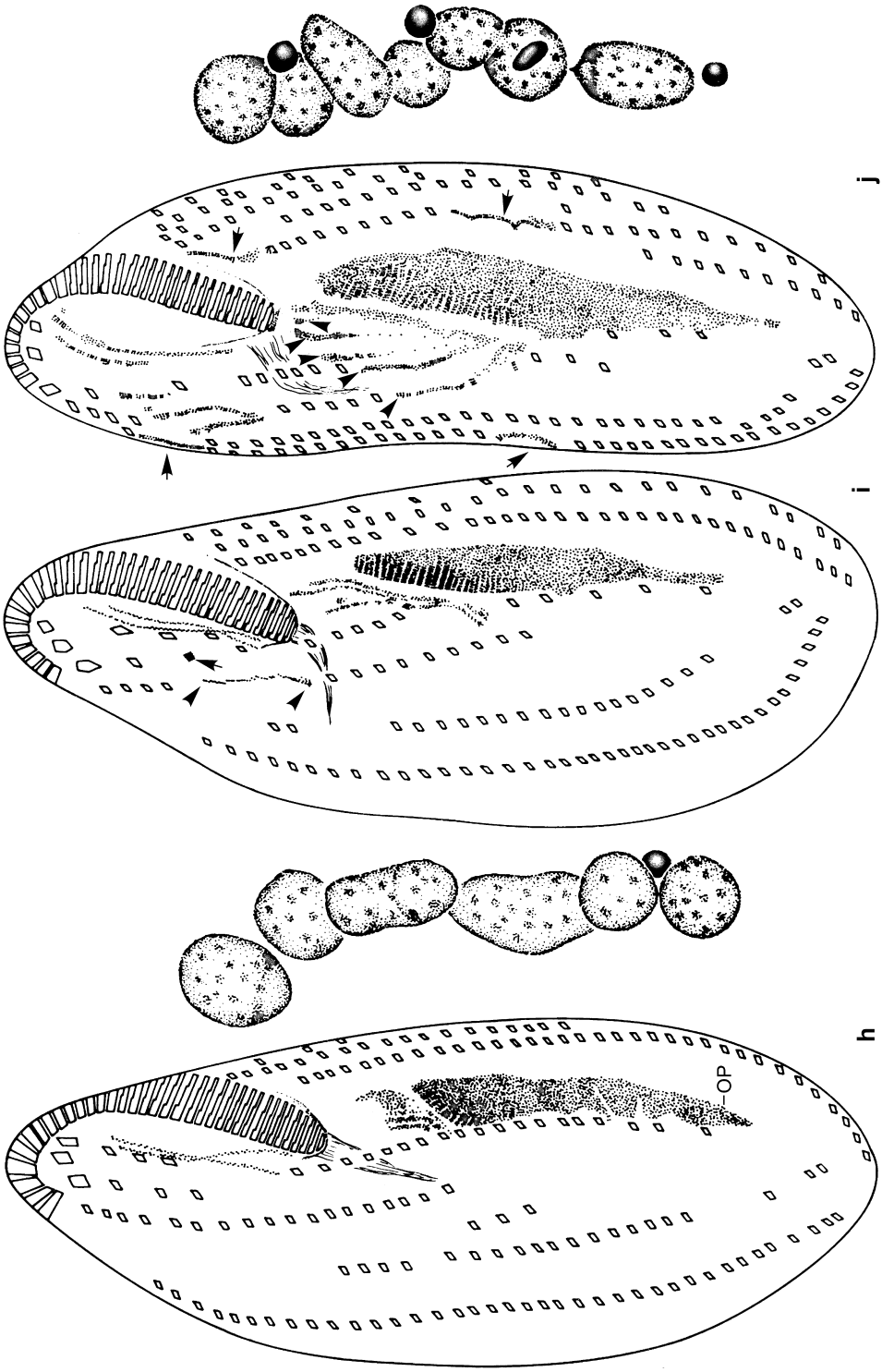


Fig. 73f, g *Parakahliella macrostoma* (from Berger et al. 1985. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus, 160 µm. Short arrow marks rear end of left frontoventral row, long arrow denotes right frontoventral row. CC = caudal cirri, 1–5 = dorsal kineties. Page 407.

Adoral zone prominent, occupies 38% of body length on average in prepared specimens, formed like a question mark with proximal end about in midline of cell and distal end at 5% of body length, that is, DE-value (Berger 2006, p. 18) about 13% in specimen illustrated (Fig. 73d); zone composed of 53 membranelles of ordi-

Fig. 73h–j *Parakahliella macrostoma* (from Berger et al. 1985. Protargol impregnation. Parental structures white, new black). Infraciliature of ventral side and nuclear apparatus of dividers. **h:** Early divider, 127 µm. **i, j:** Middle dividers, i = 131 µm, j = 130 µm. Arrow in (i) marks middle cirrus of parabuccal row, which is modified to anlage III of proter. Arrows in (j) mark marginal row primordia, arrowheads denote the (usual) five frontal-ventral cirri anlagen of the opisthe. OP = oral primordium. Page 407. →



Legend on p. 410

nary fine structure on average (Table 23). Bases of largest membranelles in life about 15 µm wide. Buccal field large and deep. Paroral and endoral slightly curved, two-rowed, intersect optically. Paroral slightly shorter than endoral, which terminates at cytopharynx; pharyngeal fibres short, but clearly recognisable in life (Fig. 73a).

Cirral pattern moderately variable, number of cirri of usual variability. Enlarged cirri about 20 µm, others 15 µm long; bases of frontal cirri about 2.7 µm in size, those of other cirri about 1.2 µm. Three enlarged frontal cirri in slightly oblique pseudorow. 3–6, on average 3.9 slightly enlarged buccal cirri right of anterior and middle portion of paroral. 3–5 slightly enlarged parabuccal cirri behind right frontal cirrus. Left frontoventral row (= cirral row 1 right of midline in original description) slightly curved leftwards, commences behind rearmost parabuccal cirrus about at 33% of body length (that is, slightly ahead of level of buccal vertex) in specimen illustrated (Fig. 73d), terminates at 96%. Right frontoventral row (= cirral row 2 right of midline in original description) begins slightly ahead of level of anteriormost parabuccal cirrus, terminates at 78% of body length; anterior cirri slightly enlarged (Fig. 73d). Transverse cirri lacking. Outer right marginal row commences on dorsal side, extends along right body margin and terminates at rear cell end, slightly separated from innermost left marginal row. Inner right marginal row commences about at 17% of body length, terminates at 83% in specimen illustrated (Fig. 73d). Four or five left marginal rows, become shorter posteriorly from inside to outside; innermost row distinctly J-shaped; outermost row laterally arranged, cirri widely spaced and slightly enlarged because they are from the previous generation(s) (see cell division). Distance between individual cirri of long marginal rows increases not or only slightly from anterior to posterior; distances in ventral rows and the middle left marginal rows in posterior third about twice as large as in anterior third. Relatively often individual cirri slightly displaced laterally.

Dorsal cilia about 5 µm long in life, invariably arranged in five kineties. Kineties 1, 3, and 5 slightly shortened anteriorly; Kineties 1 and 2 extend left of midline, kineties 3–5 right of midline (Fig. 73e). Kinety 4 distinctly shortened at both ends, with rather widely spaced basal body pairs because it is a remnant from the previous generation (see cell division). Kinety 5, a dorsomarginal kinety, terminates ahead of mid-body. In total five caudal cirri on average, about 20 µm long and therefore distinctly projecting beyond rear cell end. Usually three cirri at rear end of kinety 1 and two cirri on kinety 2.

Further and deviating observations from other populations: the live aspect of the alpine population studied by Berger et al. (1985) agrees largely with that of the type population. However, during diastole the contractile has not only an anterior canal, but also a posterior. In addition, the small crystals do not only occur close beneath the pellicle, but also in the remaining cytoplasm. Often, additional cirral rows occur to the right or to the left of the right frontoventral row. Posterior ends of marginal rows sometimes nearly confluent. Outer right marginal row usually longer than inner one, often extending onto dorsolateral surface anteriorly. Innermost left marginal

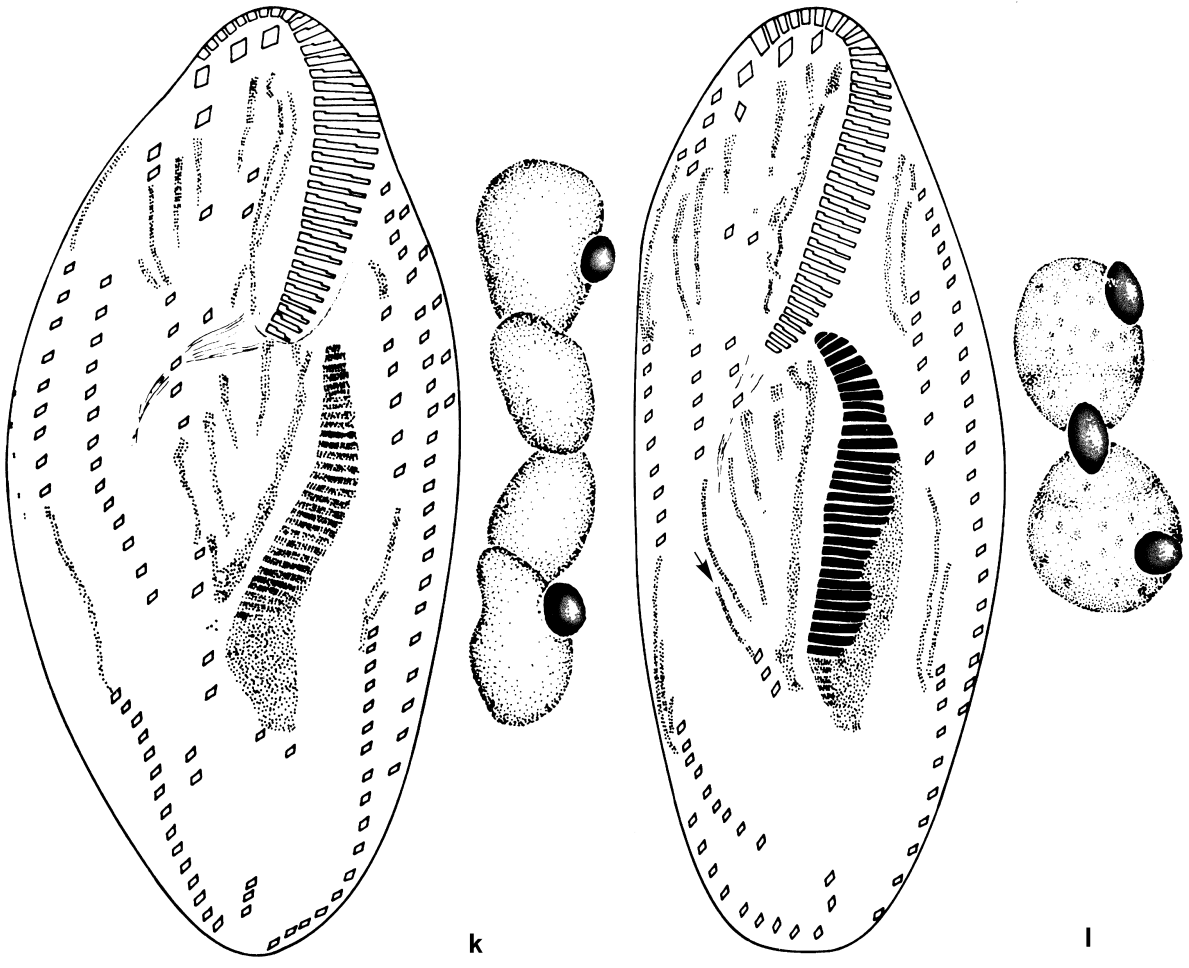
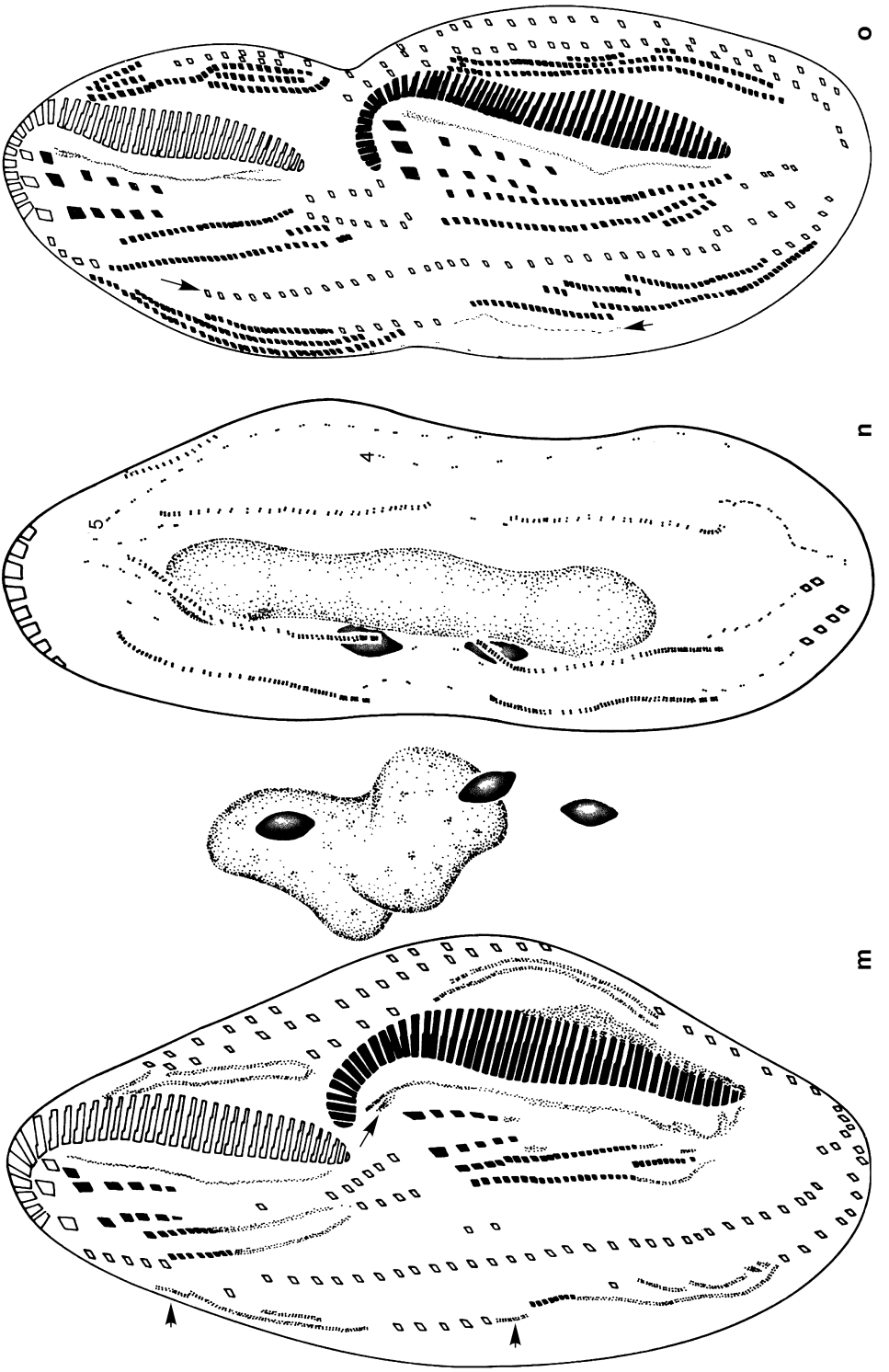


Fig. 73k, l *Parakahliella macrostoma* (from Berger et al. 1985. Protargol impregnation. Parental structures white, new black). Infraciliature of ventral side and nuclear apparatus of dividers. **k:** Middle divider, 115 µm. Usually each five frontal-ventral cirri anlagen are formed both in the proter and the opisthe. However, relatively often some additional primordia are present. **l:** Middle divider, 107 µm. Arrow marks an additional frontoventral streak. Note that the marginal primordia originate in the outer right and the inner left marginal row and form at least two rows each. Page 407.


o
n
4
5
m

row longer than next row; outermost left marginal rows are most frequently parental fragments with enlarged distances between cirri. Rarely specimens with only five macronuclear nodules (Fig. 73f, g, Table 23).

Cell division (Fig. 73h–q): Morphogenesis of cell division was studied by Berger et al. (1985).

The first morphogenetic event is the formation of an oral primordium just left of the middle and posterior portion of the frontoventral row IV (Fig. 73h). At the right anterior part of this primordium, the development of membranelles has already started. Just anteriorly, a small anarchic field is formed. This and some disorganised cirri of the middle part of the left frontoventral row shape a ramified primordium (Fig. 73i). The second (= middle) parabuccal cirrus also commences with the formation of a primordium (Fig. 73i, arrow), showing that this cirrus is homologous with cirrus III/2 of the 18-cirri hypotrichs (see Table 4 in Berger et al. 1985, and Berger 1999). From about this level posteriorly just to the end of the adoral zone some cirri of the right frontoventral row are modified to a streak (Fig. 73i, arrowheads). Membranelles of the opisthe's adoral zone organise in a posteriad direction. Simultaneously, the proliferation of new basal bodies occurs a two levels in the dorsal kineties 1, 2, and 3. The nuclear apparatus is unchanged.

The origin of the frontal-ventral primordia for the proter is as follows: anlage I from undulating membranes; anlage II from some or all buccal cirri; anlage III from second parabuccal cirrus; anlagen for left and right long frontoventral row, respectively, from some cirri of anterior part of right frontoventral row. The primordia of the opisthe originate as follows: anlage I from oral primordium and middle part of left frontoventral row; anlagen II and III from oral primordium; anlage for left frontoventral row from middle part of left frontoventral row; anlage for right frontoventral row from posterior part of right frontoventral row. Some cirri behind the anteriormost cirri of the outer right and the anteriormost cirri of the inner left marginal row are modified to the proter's marginal primordia (Fig. 73j). The middle regions of the same rows are already incorporated in the primordia of the opisthe. The oral primordium is not far advanced in the formation of membranelles.

Cell division continues with the maturation of the primordia (Fig. 73k). Both in the proter and in the opisthe five frontal-ventral cirri anlagen are recognisable. Occasionally, an additional streak occurs to the right or to the left of streak V (Fig. 73i–k, m). Presumably it forms those cirri that appear between or on the right of the

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← **Fig. 73m–o** *Parakahliella macrostoma* (from Berger et al. 1985. Protargol impregnation. Parental structures white, new black). Infraciliature of ventral side (m, o) and dorsal side (n) and nuclear apparatus of dividers. **m:** Late divider, 120 µm. Short arrows mark dorsomarginal kineties originating at/near anterior end of right marginal primordium. Long arrow denotes frontoventral anlage I of opisthe, which forms, as is usual, the left frontal cirrus. **n:** Late divider, 103 µm. The parental dorsal kineties 4 and 5 are retained and become the "new" dorsal kinety 4 in both filial products. Kineties 1–3 are formed by intrakinetal proliferation (long anlagen) while kinety 5 originates dorsomarginally (e.g., short arrows in m). **o:** Late divider, 158 µm (dorsal side see Fig. 73p). Long arrow marks parental inner right marginal row, short arrow denotes dorsomarginal kinety of opisthe. 4, 5 = parental dorsal kineties 4 and 5. Page 407.

frontoventral rows. The marginal primordia become longer due to incorporation of parental cirri. However, none originate within the inner right and the outer left marginal rows. The macronuclear nodules begin to fuse.

A conspicuous morphogenetic event is the occurrence of additional streaks within each marginal primordium (Fig. 73l). They form the inner right and the outer left marginal row respectively. About a quarter of the adoral zone of the opisthe is still unstructured. The fusion of the macronuclear nodules is almost completed.

Cell division proceeds with the cirral segregation from the frontoventral and marginal primordia (Fig. 73l). The undulating membranes are fused in both filial products. The right half of the primordium of the adoral zone is clearly modified to the final number of membranelles, while the posterior region of the left one is still undifferentiated. The anteriormost parental cirrus of the outer right marginal row and the one in front of the opisthe's right marginal primordium are modified to primordia of the dorsomarginal kineties (Fig. 73m). Subsequently, these streaks migrate onto the dorsal surface while continuing with the proliferation of new basal bodies (Fig. 73n). The new dorsal kineties 1–3 obviously originate via intrakinetal anlagen within the parental rows 1, 2, and 3. Caudal cirri are formed at the end of the new kineties 1 and 2. The macronucleus and the micronuclei begin stretching (Fig. 73n).

By the time the segregation of new cirri is finished, the adoral zone of the opisthe has its definite shape (Fig. 73o). The new cirral rows start the extension and migration to form the mature cirral pattern. Some of the new marginal rows are still fragmentary. The parental inner right and outer left marginal row(s) – they do not produce primordia – and short fragments of the parental ventral rows are still preserved. The old dorsal kineties 1–3 are nearly completely resorbed, while the kineties 4 and 5 are fully maintained (Fig. 73n, p). They form the new kinety 4 of the opisthe and the proter respectively. To get the typical kinety pattern of a non-dividing specimen both parental kineties have to migrate in a posteriad direction (Fig. 73g). This is the only way to explain the origin of the "new" dorsal kinety 4 in both filial products. The arithmetic mean of the number of basal body pairs in kinety 4 is significantly smaller ($P<0.001$; one-sided t-test; Berger et al. 1985, p. 308) than that of kinety 5. This indicates the resorption of some few units (Table 23). Both the cell and the macronucleus are distinctly dumbbell-shaped. The divided micronuclei are still connected by a thin filament (Fig. 73p).

The last conspicuous process is the migration of the left frontoventral row to its definitive site behind the short parabuccal row of anlage III (Fig. 73q). In both filial products the streak of the undulating membranes begins to separate. A cytopharynx is not recognisable either in the proter or in the opisthe. Both possess two new right and two new left marginal rows. Occasionally, additional short new marginal rows can be observed. Most of the parental left marginal infraciliature is resorbed, but a variable fraction is preserved in the postdividers. The division of the macronuclear nodules and the mitosis of the micronuclei is still going on (Fig. 73q).

Occurrence and ecology: *Parakahliella macrostoma* is likely confined to terrestrial habitats. Type locality is a farmed and periodically flooded field (189 m above

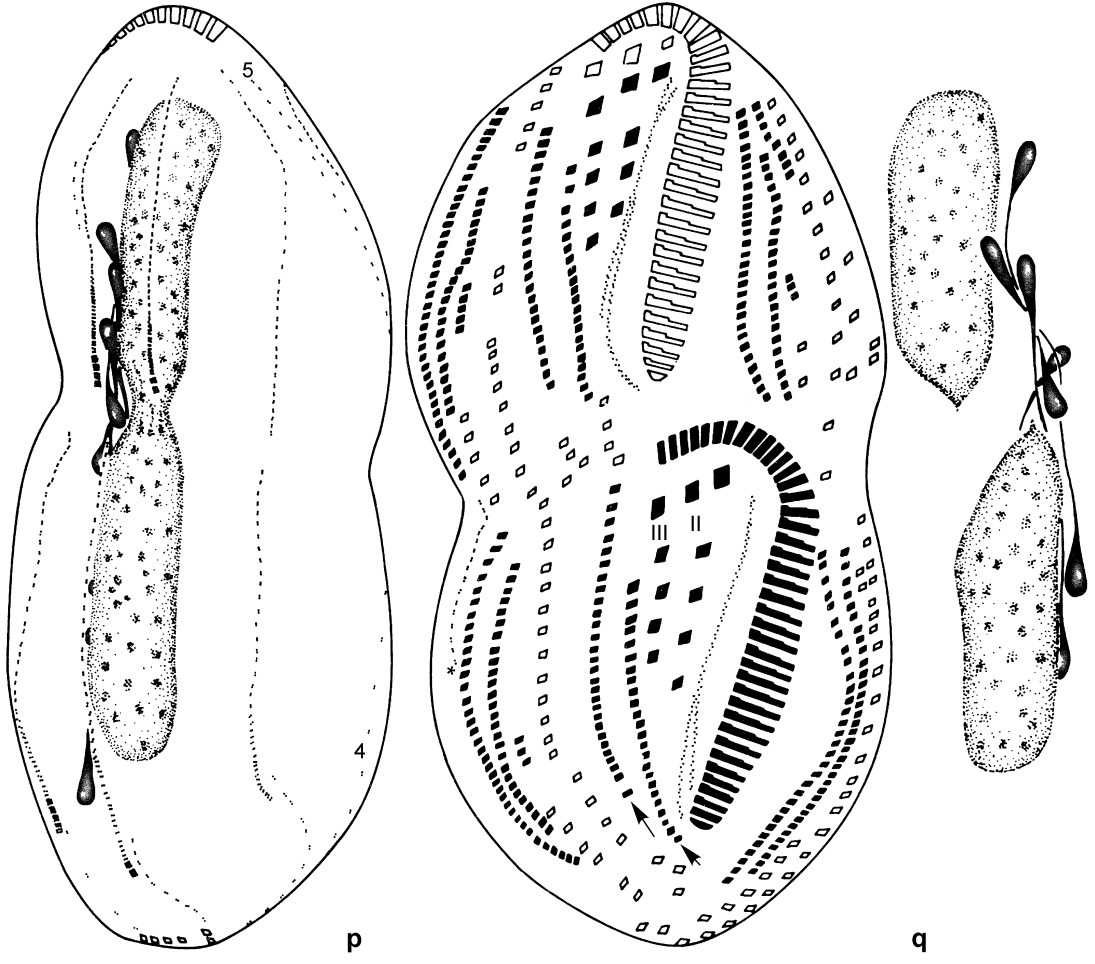

Fig. 73p, q *Parakahliella macrostoma* (from Berger et al. 1985. Protargol impregnation. Parental structures white, new black). Infraciliature of dorsal side (p) and ventral side (q) and nuclear apparatus of dividers. **p:** Late divider, 158 µm (ventral side see Fig. 73o). This stage clearly shows that dorsal kineties 1–3 are newly formed intrakinetally, whereas parental kineties 4 and 5 survive to form the "new" kinety 4 of the proter (5) and the opisthe (4). The new kinety 5 originates dorsomarginally. **q:** Very late divider, 118 µm. Short arrow marks left frontoventral row of opisthe, long arrow marks right frontoventral row of opisthe. Asterisk denotes the dorsomarginal kinety (= kinety 5) of the opisthe. Note the two new left marginal rows, a main difference to *P. haideri*, which has (usually) only one left marginal row. II, III = cirral rows formed by anlagen II and III, 4, 5 = parental dorsal kineties 4 and 5. Page 407.

sea level) near the village of Grafenwörth in Lower Austria (Foissner 1982). The population studied by Berger et al. (1985) is from a soil sample (0–2 cm) from a graded ski trail in the Schloßalm area (altitude 1950 m; collected on 1982 Aug 11) near the village of Bad Hofgastein, Austria (for detailed description of this site, see "Taxotop H" in Foissner & Peer 1985). Further records: litter underneath blueberry bush (altitude about 1200 m) from the southern face of the mountain Kammererköpfl (47°24'16"N 13°10'25") near the city of Bischofshofen, Austria (own observations); terrestrial moss from stones from the embankment of a brook (Garstnerbach) in a small village ("Höllsiedlung"), Upper Austria (own observations); floodplain soil (calcaric fluvisol) from the "Beugenau", a wetland area between the Danube river and the Vienna International Airport, Lower Austria (Foissner et al. 2005, p. 630); three sites from reclaimed, opencast coal mining area near the city of Görlitz, Germany, namely (i) 2–3 cm fresh and fermented litter layer, mainly from popular, beech, and acacia, (ii) mosses from the soil surface, and (iii) upper 3–4 cm black moder (Foissner 2000a, p. 259); experimental site of the NERC Soil Biodiversity Thematic Programme, at the Macaulay Land Use Research Institute's Sourhope Research Station, near Kelso in Southern Scotland (Finlay et al. 2001, p. 362; see also Esteban et al. 2006, p. 142); soil from fields of a farm in Ostrov near the village of Pieštany, Slovakia (Tirjaková 1988, p. 500; see also Matis et al. 1996, p. 16); soil from oak-hornbeam forest ecosystem in Southwest Slovakia (Holecová et al. 2005, p. 214); tree-holes of *Acer campestre* and *Quercus dalechampii* from the Malé Karpaty Mountains in Slovakia (Tirjaková & Vdačný 2005, p. 26).

Parakahliella macrostoma feeds on naked amoebae and ciliates, for example, *Pseudochilodonopsis mutabilis*, but also on desmidiaceans, like *Cylindrocystis* sp. Food-ciliates were caught while *P. macrostoma* is swimming and ingested very rapidly (Foissner 1982, Berger et al. 1985). Biomass of 10^6 specimens 168 mg (Foissner 1987a, p. 125; 1998, p. 207)[1].

Parakahliella terricola (Buitkamp, 1977) Berger, Foissner & Adam, 1985

(Fig. 74a, b, Table 23)

1977 ***Paraurostyla terricola* n. spec.** – Buitkamp, Decheniana, 130: 118, Abb. 2 (Fig. 74a, b; original description; no formal diagnosis provided and site where type slides are deposited not mentioned; see nomenclature).

1985 ***Parakahliella terricola* (Buitkamp, 1977) nov. comb.** – Berger, Foissner & Adam, Protistologica, 21: 309 (comparison with *P. macrostoma* and combination with *Parakahliella*).

2000 ***Fragmocirrus terricola* (Buitkamp, 1977) nov. comb.** – Foissner, Stud. Neotrop. Fauna & Environm., 35: 68 (combination with *Fragmocirrus*).

[1] Foissner (1987a, 1998) quote a rather different biomass for *P. macrostoma* (168 mg per 10^6 specimens) and *P. terricola* (504 mg), respectively, although the body size is similar. It is recommended to calculate the biomass for each population individually.

2001 ***Parakahliella terricola* (Buitkamp, 1977) Berger, Foissner and Adam, 1985** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 70 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).

Nomenclature: No derivation of the species-group name *terricola* is given in the original description. It is a composite of the Latin noun *terr·a* (soil), the thematic vowel *·i-*, and the Latin verb *colere* (to live in) and means living in soil, the habitat where the species was discovered. Usually, species-group names ending with *-cola* are considered as appositive substantives and are thus not changed when transferred to a genus of different gender (Werner 1972, p. 138). Foissner (1987a, p. 126; 1998, p. 207) incorrectly dated the paper by Berger et al. (1985) with 1986.

The type slides are likely deposited in the "Institut für landwirtschaftliche Zoologie und Bienenkunde" of the University of Bonn (Germany), where Buitkamp worked.

Esteban et al. (2006, p. 142) mentioned the present species under "*Parakahliella (Paraurostyla) terricola*" which would mean that they consider *Paraurostyla* as subgenus of *Parakahliella* (ICZN 1999, Article 6.1). However, likely they intended to say that this species was previously/originally assigned to the genus *Paraurostyla*.

Remarks: Buitkamp (1977) found this species in a soil sample in Germany and described it mainly (exclusively?) after protargol preparations. It closely resembles *Paraurostyla macrostoma*, which was described by Foissner (1982). Foissner distinguished the two species by the following features: (i) subpellicular crystals lacking in *P. terricola* versus present in *P. macrostoma*. According to Foissner (1982), the crystals cause a light yellow-brownish colour. Consequently, it cannot be excluded that *P. terricola* also has such crystals because Buitkamp (1977) mentioned a brownish colour too; (ii) number of adoral membranelles (28 [single value] vs. 53 on average [range 38–61]). This is indeed a rather conspicuous difference, especially for populations whose specimens have about the same body size. It is very unlikely that Buitkamp (1977) underestimated (incorrectly counted?) the number so distinctly; (iii) number of caudal cirri (3 [single value] vs. 5 on average [range 4–6]). Unfortunately, nothing is known about the distribution of the caudal cirri per kinety in *P. terricola*; (iv) "fragmentation" of frontoventral rows (strong [Fig. 74a] vs. weak [Fig. 73d]). Generally, one has the impression that *P. terricola* has a lower total number of cirri than *P. macrostoma*; (v) number of left marginal rows (3 [single value?] vs. 4.2 on average [range 4 or 5]). The difference is not very distinct inasmuch as nothing is known about the variability of this feature in *P. terricola*.

In 1985, we established *Parakahliella* and designated *Paraurostyla macrostoma* as type species (Berger et al. 1985). Simultaneously, we transferred the present species to *Parakahliella* and again discussed the differences between these two species (Berger et al. 1985, p. 309). Our criteria for the discrimination of *P. macrostoma* from *P. terricola* were again the mean number of adoral membranelles (nearly twice as high, and even the minimum value is considerably higher), the less fragmented frontoventral and right marginal rows, and the possession of small crystals. In addition, the number of caudal cirri is perhaps lower in *P. terricola* than in *P. macro-*

stoma (3 vs. 5). Since new data are lacking, I preliminary retain our previous decision. To clear up the question whether or not *P. macrostoma* is a synonym of *P. terricola* detailed studies (morphological, genetical, molecular biological) on populations from the type localities are needed. The present species can be easily distinguished from *P. haideri* by the number (3 vs. 1) of left marginal rows (Berger & Foissner 1989b; see key to species).

Foissner (2000) established *Fragmocirrus* for a species which closely resembles *Parakahliella* spp. The main difference is the lack of transverse cirri in *Parakahliella*. In addition, *Parakahliella* preserves a parental dorsal kinety. *Parakahliella terricola* has usually two cirri left of the posterior end of the right marginal row; sometimes these cirri are lacking (Fig. 74a). Since they are somewhat smaller (3 × 3 cilia) than the other ventral and marginal cirri (4 × 3 cilia), Buitkamp (1977) supposed that these are transverse cirri. Foissner (2000) accepted this designation and therefore transferred *P. terricola* to *Fragmocirrus*. By contrast, I prefer the present classification because I suppose that these two cirri are not transverse cirri, which are usually larger than or at least of the same size as the ventral and marginal cirri, and – more important – they usually form an oblique pseudorow. In *F. espeletiae* the transverse cirri are true transverse cirri, respectively, pretransverse ventral cirri as indicated by the distinct migration to the posterior body portion (Fig. 64 in Foissner 2000). In *P. terricola* one cannot exclude that these two cirri are parental cirri, a fact which would explain the somewhat smaller size due to a resorption of some basal bodies (Fig. 74a). In addition, when the transfer of *P. terricola* to *Fragmocirrus* is accepted, then *P. macrostoma* also has to be transferred to *Fragmocirrus* because this species also has often – like *P. terricola* – one or two cirri left of the rear end of the right marginal row (Fig. 73d, f). However, since *P. macrostoma* is the type species of *Parakahliella* Berger, Foissner & Adam, 1985, *Fragmocirrus* Foissner, 2000 would be superfluous. Furthermore, *Parakahliella terricola* has, like *P. macrostoma*, five dorsal kineties (likely also including a dorsomarginal kinety and one parental row), whereas *F. espeletiae* has only four kineties, because it lacks a parental row. For further discussion, see remarks at genus section.

Morphology: Body length 150–200 µm in life(?); body length:width ratio of specimen illustrated 2.7:1 (Fig. 74a). Body outline elliptical, anterior end broadly rounded, posterior end narrowly rounded. Macronucleus left of median, moniliform, that is, eight ellipsoidal nodules necklace-like arranged. Four micronuclei. Contractile vacuole near left cell margin at about 44% of body length (Fig. 74a). Consistency of body (flexible [likely], rigid), presence/absence of cortical granules, and/or special cytoplasmic inclusions not mentioned; however, body brownish (unfortunately, cause not mentioned; see remarks). Movement not described.

Adoral zone occupies about one third of body length (30% in specimen illustrated), composed of 28 membranelles of ordinary fine structure; 28 is a rather low value for such a large species and a main difference to *P. macrostoma* (see remarks). Buccal area wide. Undulating membranes distinctly curved, about of equal length, optically intersecting, both double-rowed (Fig. 74a).

Cirral pattern as shown in Fig. 74a; variability not well documented, thus most data refer to the specimen illustrated (Table 23). Three strong frontal cirri arranged in oblique pseudorow. Three slightly enlarged buccal cirri right of anterior and middle portion of undulating membranes. Two parabuccal cirri behind right frontal cirrus. Left frontoventral row about in median of cell, commences near buccal vertex, terminates at 68% of body length, composed of nine cirri. Right frontoventral row commences left of right frontal cirrus, terminates at 44% of body length, composed of 12 cirri. One short row in rear body portion composed of 4–5 cirri (whether this is the rear, dislocated portion of the right frontoventral row or a fragment of a parental row is not known). Inner right marginal row, as in *P. macrostoma*, left of middle portion of outer right marginal row, anteriorly and posteriorly strongly shortened and thus composed of 12 cirri only. Left of rear end of outer right marginal row usually two cirri (lacking in some specimens), which are, according to Buitkamp (1977), perhaps transverse cirri because they consist of only 3 × 3 cilia whereas the ventral and marginal cirri are composed of 4 × 3 cilia (Fig. 74a); I suppose that these two cirri are not transverse cirri, but cirri from the previous generation (details see remarks). Outer right marginal

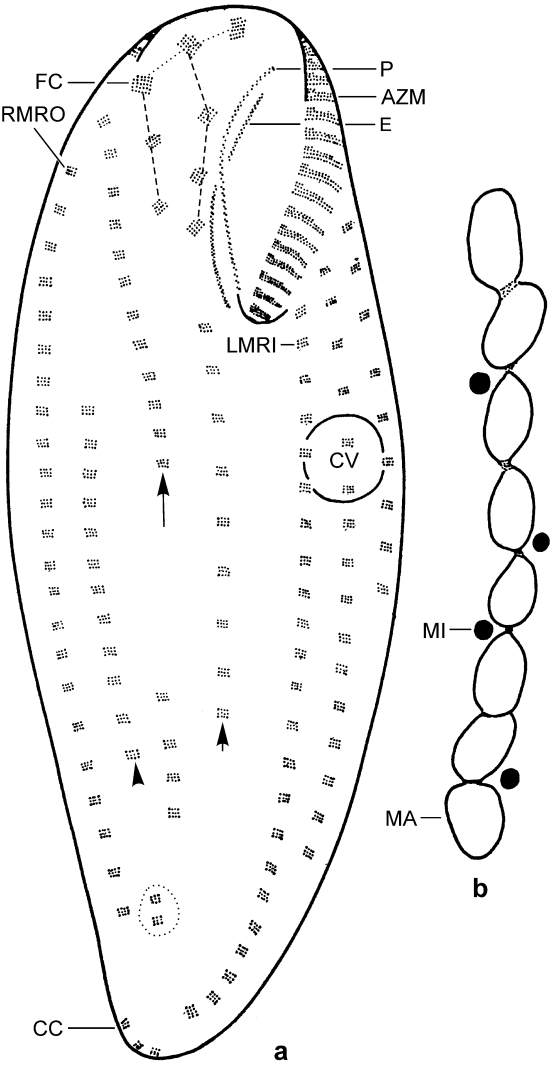

Fig. 74a, b *Parakahliella terricola* (from Buitkamp 1977. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus, 167 µm. Dotted line connects frontal cirri; broken lines connect cirri which originate from same anlage (only shown for anlagen II and III). The two cirri circled by a dotted line are, according to the original description, transverse cirri (see remarks for details). Short arrow denotes rear end of left frontoventral row, long arrow marks right frontoventral row. Arrowhead marks rear end of inner right marginal row. AZM = adoral zone of membranelles, CC = caudal cirri, CV = contractile vacuole, E = endoral, FC = right frontal cirrus, LMRI = inner left marginal row (= left marginal row 1), MA = macronuclear nodule, MI = micronucleus, P = paroral, RMRO = outer right marginal row. Page 418.

row distinctly shortened anteriorly, that is, commences at 15% of body length in specimen illustrated, terminates at 86% of body length. Three left marginal rows (Fig. 74a), composed of 23 (inner row), 16 (middle), and nine (outer) cirri. All cirri on ventral side about 20 µm long.

Dorsal bristles 5 µm long, arranged in five kineties; unfortunately, no details about arrangement given. However, the high similarity of the ventral cirral pattern of *Parakahliella terricola* and *P. macrostoma* indicates that the dorsal pattern and its morphogenesis are also very similar or even identical. Three caudal cirri at tip of rear cell end; each about 25 µm long; arrangement of cirri (one kinety with two cirri and one kinety with one cirrus? or three kineties with each one cirrus?) not described.

Cell division: According to Buitkamp (1977), the left frontoventral row provides the basal bodies for the oral primordium.

Occurrence and ecology: *Parakahliella terricola* is likely confined to terrestrial habitats (Foissner 1987a, p. 126; 1998, p. 207). Its type locality is the Venusberg (Melbtal), a small mountain near the city of Bonn, Germany, where Buitkamp (1977) discovered it in a soil sample (soil type brown earth) of a pasture dominated by *Poa annuae*, *P. pratensis*, *Lolium perenne*, *Taraxacum officinale*, and *Trifolium repens*. Further records: experimental site of the NERC Soil Biodiversity Thematic Programme, at the Macaulay Land Use Research Institute's Sourhope Research Station, near Kelso in Southern Scotland (Finlay et al. 2001, p. 363; not distinguished from *P. macrostoma*; see also Esteban et al. 2006, p. 142); Antarctic soil (Sudzuki 1979, p. 123; not substantiated by morphological data).

Parakahliella terricola feeds on ciliates (Buitkamp 1977). Biomass of 10^6 specimens 504 mg (Foissner 1987a, p. 126; 1998, p. 207); according to Buitkamp (1979, p. 225), one specimens has a volume of 10.8×10^{-8} cm^3, which corresponds a biomass of 108 mg per 10^6 specimens (see also same topic at *P. macrostoma*).

Parakahliella haideri Berger & Foissner, 1989
(Fig. 75a–w, Table 23)

1989 ***Parakahliella haideri* nov. spec.**[1] – Berger & Foissner, Bull. Br. Mus. nat. Hist. (Zool.), 55: 11, Fig. 1–22, Table 1 (Fig. 75a–w; the holotype slide [accession number holotype N 1987:3:19:1] and a paratype slide [paratype N 1987:3:19:2] are deposited in the British Museum, Natural History, London; Berger & Foissner 1989b).

1995 ***Parakahliella haideri* Berger and Foissner, 1989** – Eigner, Europ. J. Protistol., 31: 355, Fig. 42 (Fig. 75j; redefinition of the Kahliellidae).

2001 ***Parakahliella haideri* Berger and Foissner, 1989** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 69 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).

[1] Berger & Foissner (1989b) provided the following diagnosis: In vivo about 150 × 50 µm. 1 long and 1 short (sometimes absent) right and 1 left marginal row. 48 adoral membranelles and 6 macronuclear segments on average.

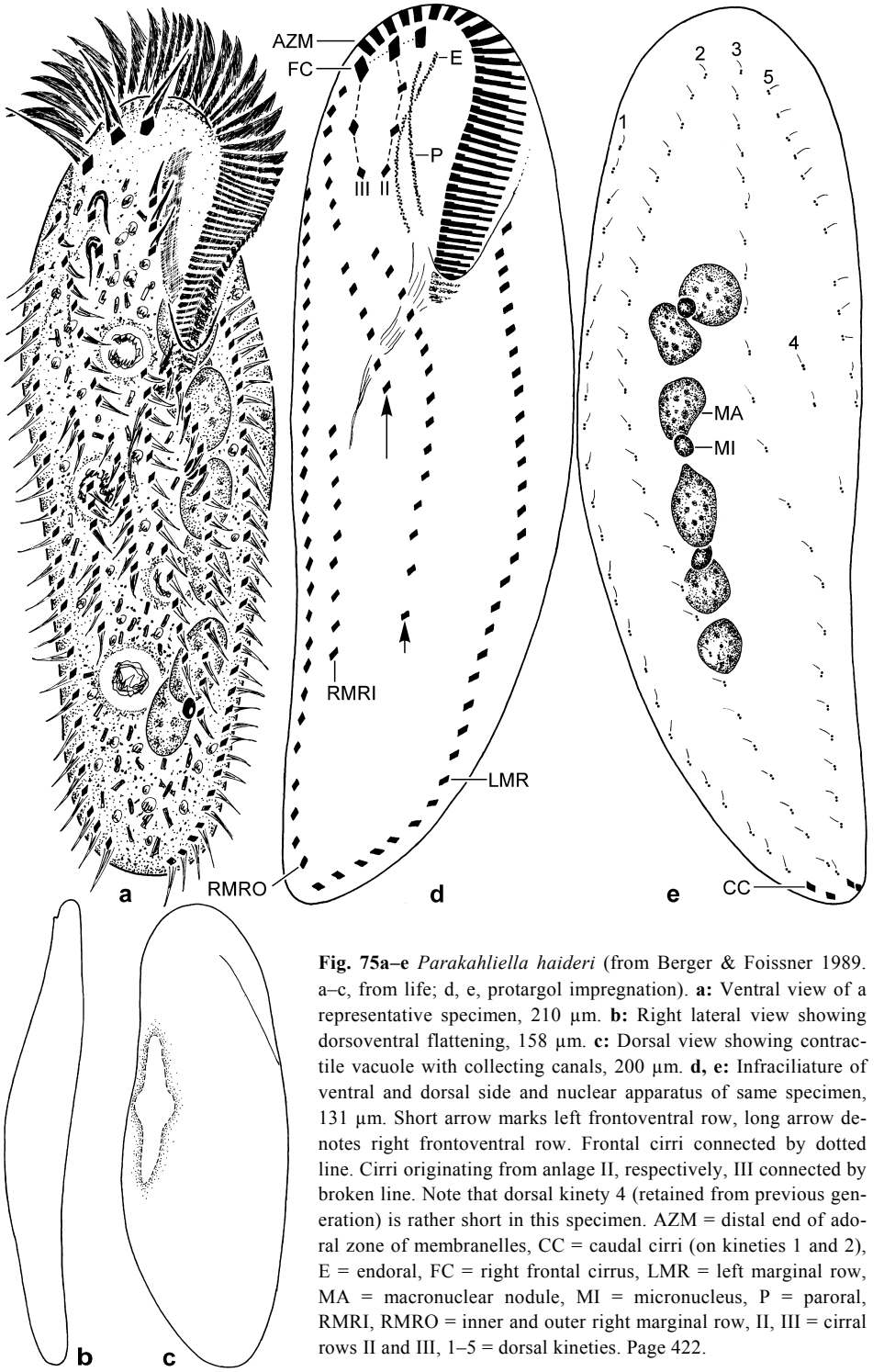

Fig. 75a–e *Parakahliella haideri* (from Berger & Foissner 1989. a–c, from life; d, e, protargol impregnation). **a:** Ventral view of a representative specimen, 210 µm. **b:** Right lateral view showing dorsoventral flattening, 158 µm. **c:** Dorsal view showing contractile vacuole with collecting canals, 200 µm. **d, e:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 131 µm. Short arrow marks left frontoventral row, long arrow denotes right frontoventral row. Frontal cirri connected by dotted line. Cirri originating from anlage II, respectively, III connected by broken line. Note that dorsal kinety 4 (retained from previous generation) is rather short in this specimen. AZM = distal end of adoral zone of membranelles, CC = caudal cirri (on kineties 1 and 2), E = endoral, FC = right frontal cirrus, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMRI, RMRO = inner and outer right marginal row, II, III = cirral rows II and III, 1–5 = dorsal kineties. Page 422.

2002 ***Parakahliella haieri*** – Lynn & Small, Ciliophora, p. 456, Fig. 49A, B (Fig. 75d, e; incorrect subsequent spelling of *haideri*; guide to ciliate genera).
2007 ***Parakahliella haideri*** – Jankowski, Ciliophora, p. 458, Fig. 290 (Fig. 75a; revision of ciliates).

Nomenclature: This species was dedicated to Reinhold Haider, director of the Hydrologische Untersuchungsstelle Salzburg.

In the original description we wrote "A slide of holotype specimens and ..." (Berger & Foissner 1989b, p. 11). This is not quite correct because only one specimen can be the holotype (ICZN 1999, Article 73.1.1). In addition, we did not fix a holotype specimen, at least not in the paper.

Remarks: *Parakahliella haideri* differs from *P. macrostoma* and *P. terricola* by the presence of only one left marginal row. There is some evidence which suggests that there is a small variation in the number of the left marginal rows, even in species with normally only one row (for review, see Berger & Foissner 1989b). However, in many morphometrical investigations this feature was shown to be very stable in natural populations. Thus, some variation might be caused by prolonged or suboptimal culture conditions and should not be overinterpreted, for example, in that they are included in species diagnosis (Berger & Foissner 1989b). In addition, *Parakahliella terricola* has a distinctly lower number of adoral membranelles than the present species (28 vs. 48 [34–62]; Table 23). All other morphometrical features overlap considerably. *Parakahliella* differs from *Afrokahliella* by the curious dorsal kinety formation, that is, the preservation of parental kineties 4 and 5. However, this feature is difficult to recognise in live specimens. *Afrokahliella binucleata* and *A. namibicola* have only two macronuclear nodules (vs. 5–9 in *P. haideri*; Table 23); further, *Afrokahliella binucleata* has distinct cortical granules (vs. absent). For a separation from *A. halophila* see there (p. 440).

Morphology: Body size in life about 150 × 50 µm; body length:width ratio thus 3:1 in life, about 2.4:1 on average in protargol preparations (Table 23). Body outline usually S-shaped, sometimes distinctly converging posteriad, both ends rounded (Fig. 75a). Body very flexible, but not contractile; about 2:1 flattened dorsoventrally (Fig. 75b). Macronuclear nodules ellipsoidal, arranged left of median (Fig. 75a, e, h). Micronuclei globular, near macronuclear nodules. Contractile vacuole, as is usual, close to left body margin, ahead of mid-body (at 41% of body length in specimen shown in Fig. 75c); during diastole with short collecting canals. Cortical granules lacking. Cytoplasm colourless, contains many yellow shining, 2–4 µm large crystals

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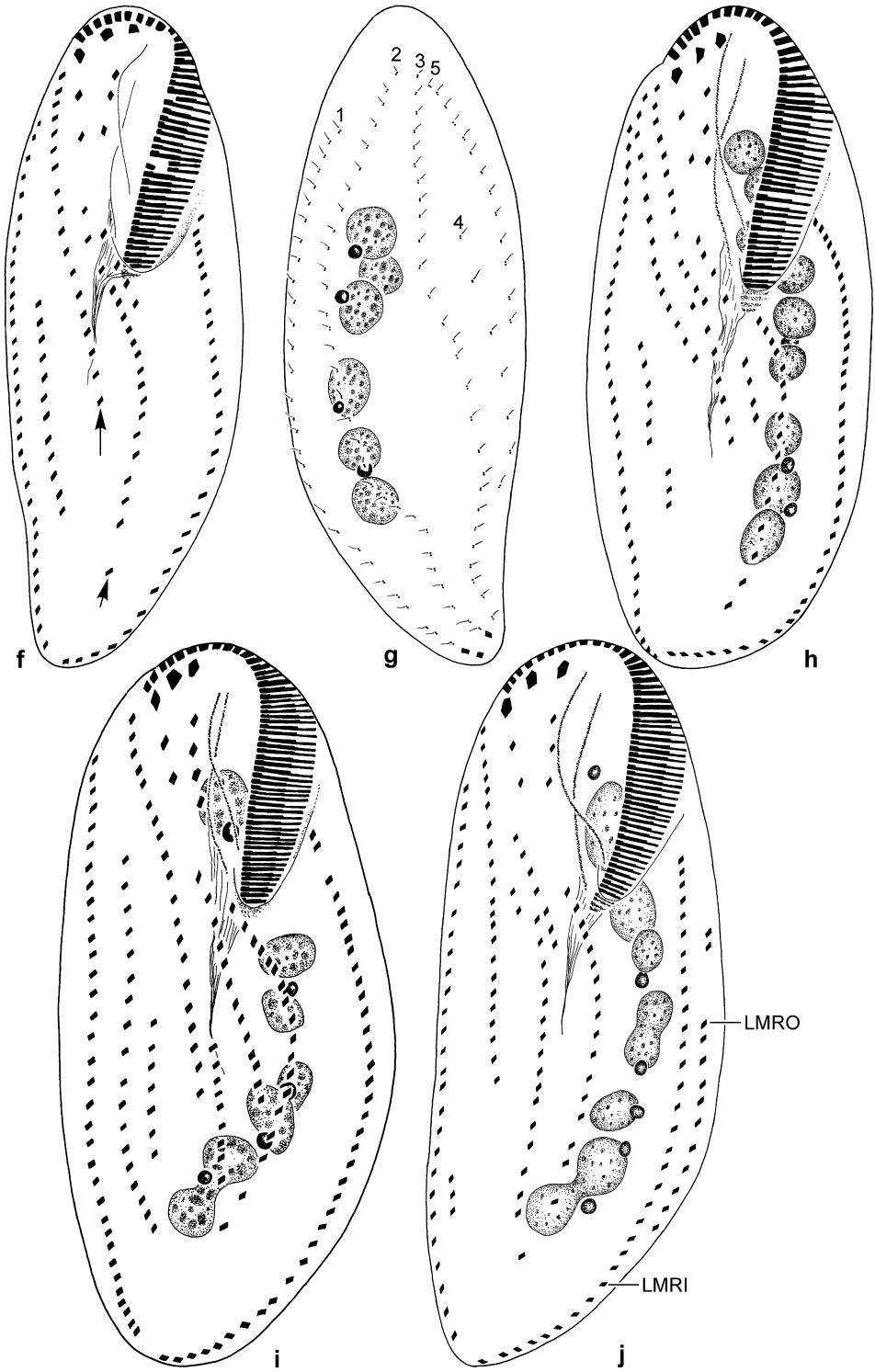
Fig. 75f–j *Parakahliella haideri* (f, original; g–j, from Berger & Foissner 1989. Protargol impregnation). → **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 123 µm. Kinety 4 has the ordinary length in this specimen. Short arrow marks rear end of left frontoventral row, long arrow denotes rear end of right frontoventral row. **h, i:** Infraciliature of ventral side and nuclear apparatus of specimens with additional cirral rows, h = 122 µm, i = 159 µm. **j:** Infraciliature of ventral side and nuclear apparatus of a specimen with a second left marginal row, 150 µm. LMRI, LMRO = inner and outer left marginal row (LMRI = left marginal row 1), 1–5 = dorsal kineties (note that kinety 4 is a parental row, that is, from the previous generation!). Page 422.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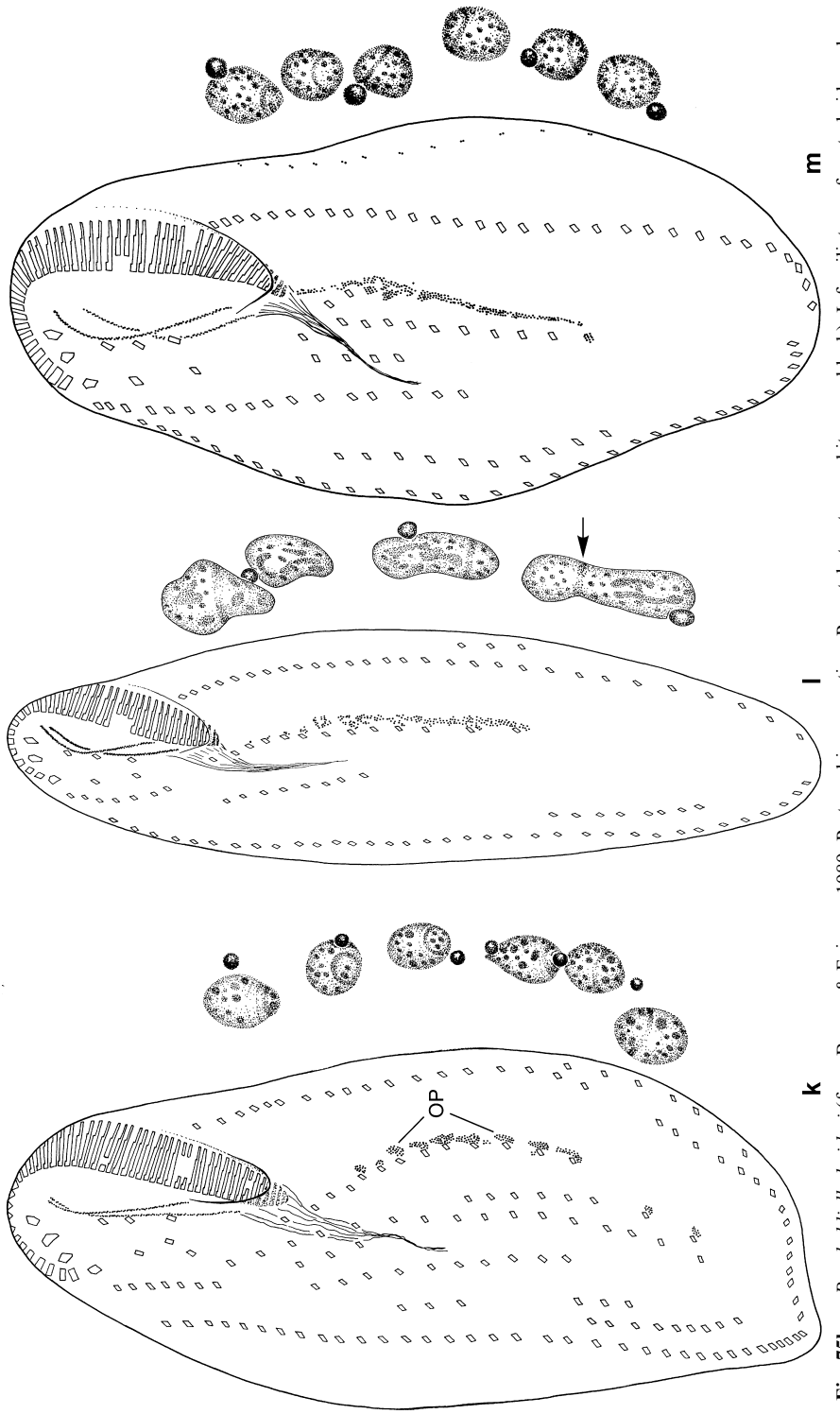


Fig. 75k–m *Parakahliella haideri* (from Berger & Foissner 1989. Protargol impregnation. Parental structures white, new black). Infraciliature of ventral side and nuclear apparatus of very early (k, l) and early (m) dividers, k = 169 µm, l = 159 µm, m = 142 µm. Arrow in (l) marks replication band of a macronuclear nodule. OP = oral primordium left of rear portion of left frontoventral row. Page 422.

and some food vacuoles. Movement without peculiarities, that is, usually moderately rapid gliding.

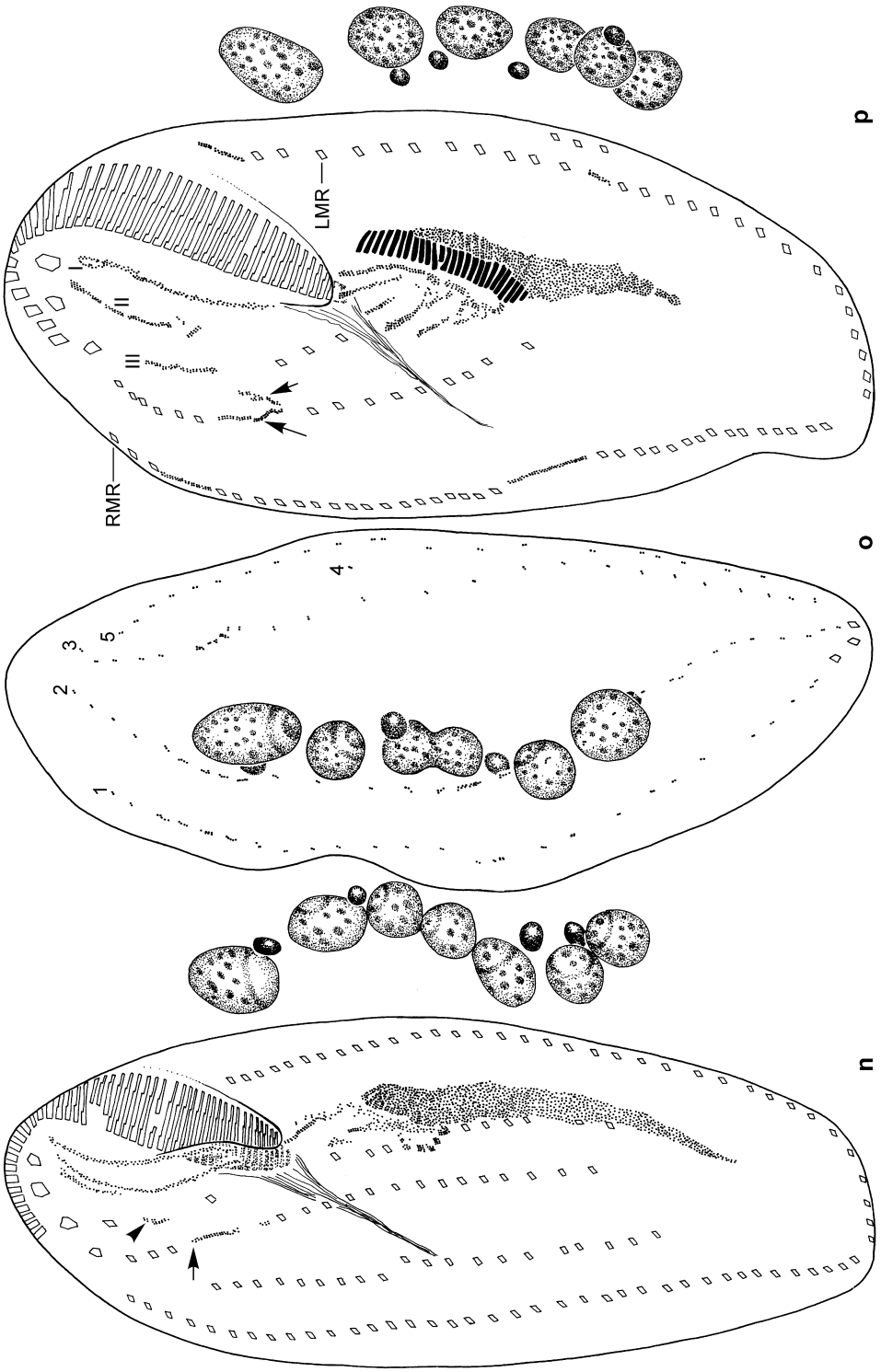
Adoral zone occupies 38% of body length on average, formed like a question mark, composed of 48 membranelles of ordinary fines structure on average (Table 23). Bases of largest membranelles about 10 µm wide in life. Buccal area deep and wide. Undulating membranes long and distinctly bent, optically intersecting; paroral usually commences slightly more anteriorly than endoral. Pharyngeal fibres extend obliquely backwards (Fig. 75a, d, f, h–j).

Cirral pattern very variable due to more or less long "additional" frontoventral rows. Unequivocal designation of rows thus difficult, respectively, impossible (Fig. 75d, f, h–j, Table 23). Three strongly enlarged frontal cirri arranged in oblique pseudorow. Buccal cirri and cirri behind right frontal cirrus (= parabuccal cirri) only slightly larger than remaining frontoventral and marginal cirri. Left frontoventral row roughly in line, but clearly separated from parabuccal cirri; commences mostly slightly ahead of level of buccal vertex, terminates in posterior half of cell (Fig. 75d). Right frontoventral row commences almost at level of right frontal cirrus, terminates usually in middle of cell. Transverse cirri lacking. Usually two right marginal rows, namely, a shorter inner, and longer outer row. Outer right marginal row distinctly shortened anteriorly; begins at 20% of body length in specimen shown in Fig. 75d; ends close to rear end of left marginal row, which begins left of proximal portion of adoral zone; marginal cirri about 15 µm long in life. Very rarely (in about one of 50 specimens) a short second left marginal row occurs (Fig. 75j). Parental cirri (marginal, frontoventral) lacking.

Dorsal cilia 2–3 µm long in life. Kinety 1 slightly shortened anteriorly, kineties 2 and 3 of body length; kinety 5, a dorsomarginal row, commences anteriorly, terminates at 44% of body length in specimen shown in Fig. 75e. Between rear portion of kinety 5 and middle portion of kinety 3 invariable a more or less long row (= kinety 4) of parental dikinetids; thus, invariable five dorsal kineties (four new and one parental) present (Fig. 75e, g). Kineties 1 and 2 with caudal cirri.

Cell division: Morphogenesis of cell division was studied in detail by Berger & Foissner (1989b). It commences with the proliferation of basal bodies immediately left of the middle and posterior part of the left frontoventral row (Fig. 75k, l). Subsequently a long and narrow oral primordium is formed (Fig. 75m). The membranelles of the opisthe's adoral zone organise, as is usual, in a posterior direction. The buccal cirri, the second parabuccal cirrus (obviously homologous with cirrus III/2 of the 18-cirri hypotrichs; see Table 4 in Berger 1999) behind the right frontal cirrus, and some cirri in the anterior part of the right frontoventral row are modified to primordia. The parental undulating membranes commence with reorganisation (Fig. 75n). At about the same time the proliferation of new basal bodies occurs at two levels within the dorsal kineties 1–3 (Fig. 75o).

Division continues with the formation of the proter's and opisthe's marginal row primordia and the further development of the frontal-ventral streaks. Usual five such streaks are formed, occasionally 6–9 occur (Fig. 75p). Cortical morphogenesis pro-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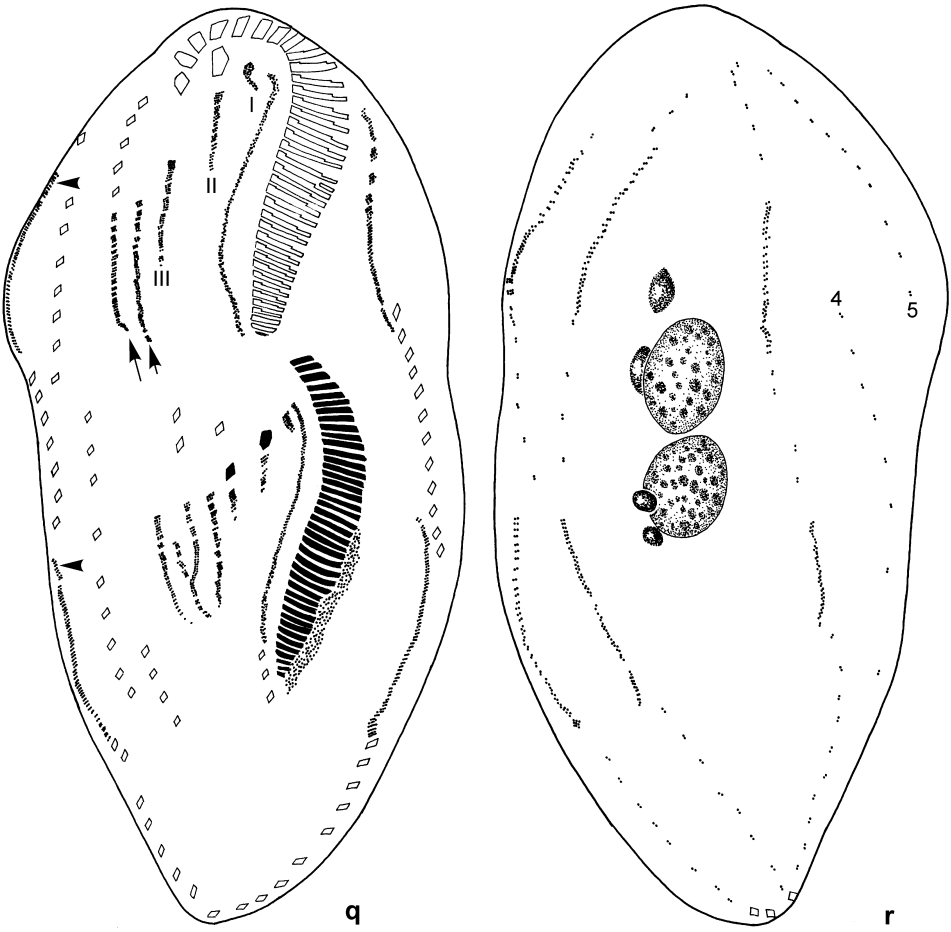


Fig. 75q, r *Parakahliella haideri* (from Berger & Foissner 1989. Protargol impregnation. Parental structures white, new black). Infraciliature of ventral and dorsal side and nuclear apparatus of middle divider, 134 µm. Short arrow marks left frontoventral row, long arrow denotes right frontoventral row. Arrowheads mark anlagen for dorsomarginal kineties. Within dorsal kineties 1–3 each two anlagen originate, that is, one for the proter and one for the opisthe; parental kineties 4 and 5 are retained and form the "new" kinety 4 of the proter (parental kinety 5) and the opisthe (parental kinety 4). The new dorsal kinety 5 is formed dorsomarginally (see q). I–III = anlagen I (forming left frontal cirrus), II (middle frontal cirrus and buccal cirri), and III (right frontal cirrus and parabuccal cirri), 4, 5 = parental dorsal kineties 4 and 5. Page 422.

← **Fig. 75n–p** *Parakahliella haideri* (from Berger & Foissner 1989. Protargol impregnation. Parental structures white, new black). **n:** Infraciliature of ventral side and nuclear apparatus of an early divider, 159 µm. Arrowhead marks anlage III of proter formed from middle parabuccal cirrus, arrow denotes the anlage which somewhat later (see p) forms the primordia for the left and right frontoventral row. **o:** Infraciliature of dorsal side and nuclear apparatus of an early divider, 142 µm. Note the anlagen in kineties 1–3. **p:** Infraciliature of ventral side and nuclear apparatus of a middle divider, 121 µm. Arrows mark V-shaped anlage of proter forming the primordia for left and right frontoventral row. LMR = left marginal row, RMR = right marginal row, II, III = anlagen for cirral rows II (middle frontal cirrus plus buccal cirri) and III (right frontal cirrus and parabuccal row), 1–5 = dorsal kineties. Page 422.

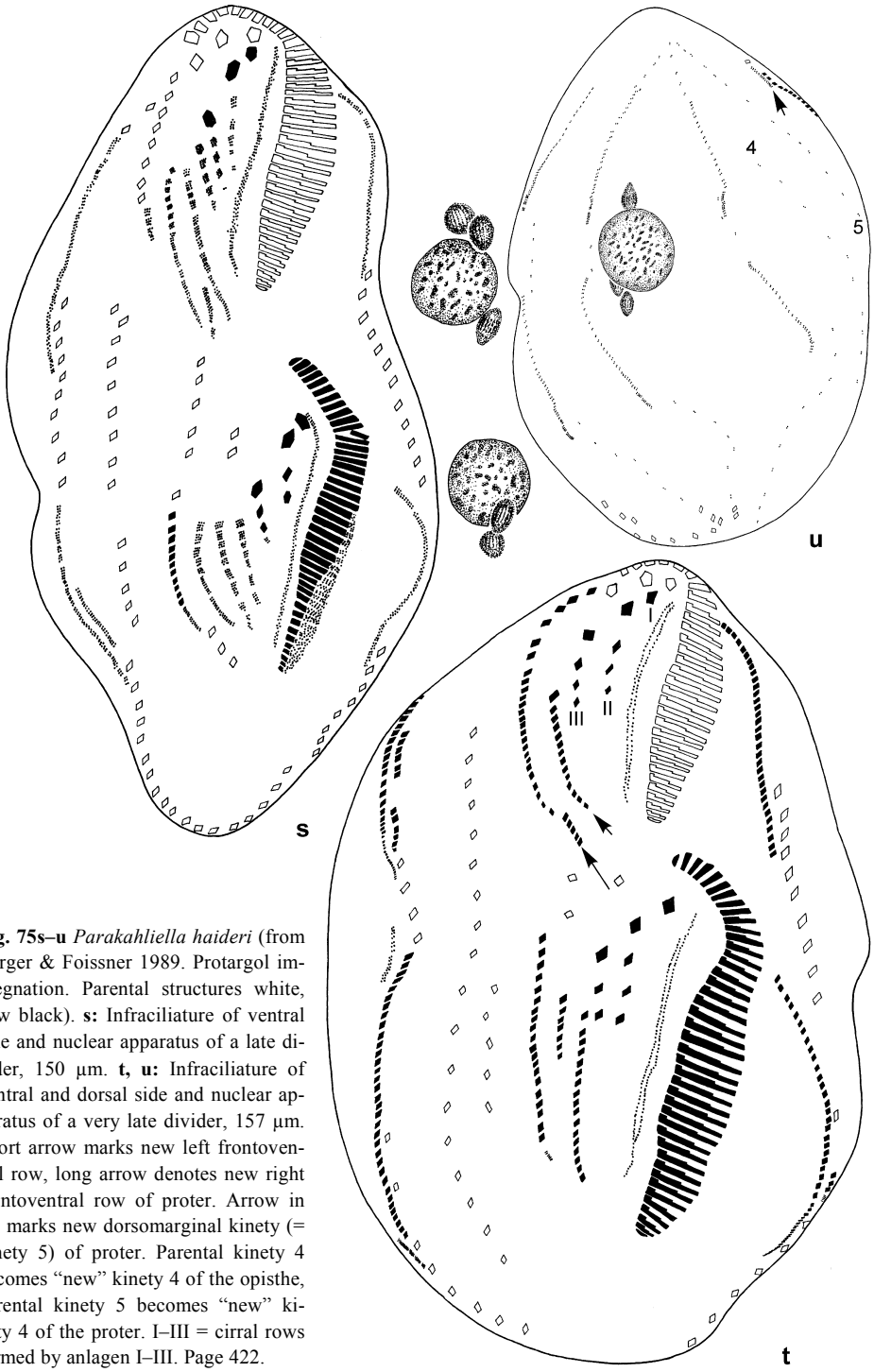


Fig. 75s–u *Parakahliella haideri* (from Berger & Foissner 1989. Protargol impregnation. Parental structures white, new black). **s:** Infraciliature of ventral side and nuclear apparatus of a late divider, 150 µm. **t, u:** Infraciliature of ventral and dorsal side and nuclear apparatus of a very late divider, 157 µm. Short arrow marks new left frontoventral row, long arrow denotes new right frontoventral row of proter. Arrow in (u) marks new dorsomarginal kinety (= kinety 5) of proter. Parental kinety 4 becomes "new" kinety 4 of the opisthe, parental kinety 5 becomes "new" kinety 4 of the proter. I–III = cirral rows formed by anlagen I–III. Page 422.

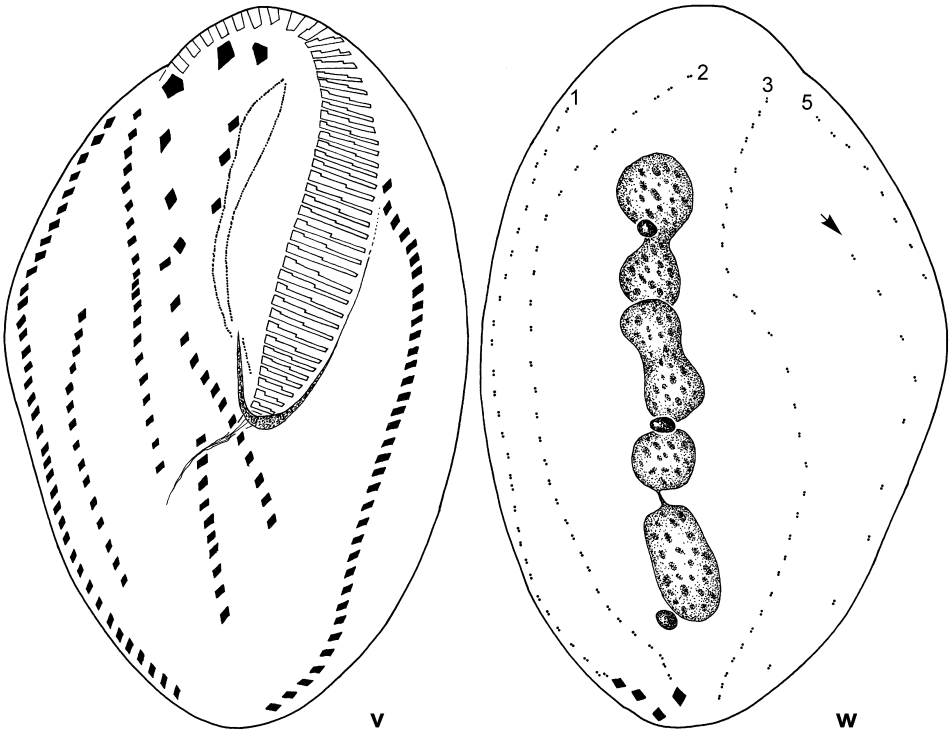


Fig. 75v, w *Parakahliella haideri* (from Berger & Foissner 1989. Protargol impregnation. Parental structures white, new black). Infraciliature of ventral and dorsal side and nuclear apparatus of rear post divider, 88 µm. Arrow in (w) marks parental kinety 4, which forms the "new" kinety 4 of this rear filial product. 1–3, 5 = newly formed dorsal kineties. Page 422.

ceeds with the cirral segregation from these streaks. At the anterior end of each right marginal primordium, one primordium for a dorsomarginal kinety is separated and migrates onto the dorsal surface (Fig. 75q, u). The primordia in the dorsal kineties 1–3 are elongated (Fig. 75r).

Figure 75s shows a late divider, where a large portion of the adoral zone of the opisthe is organised and the final number of membranelles recognisable. Many parental frontoventral and marginal cirri are still preserved. Parallel to the right marginal row of the opisthe is a short marginal streak in this specimen which forms the – usually short – inner right marginal row.

When the segregation of the frontoventral cirri is finished, the new left frontoventral row becomes displaced in a posterior direction. At this stage the undulating membranes of both the proter and the opisthe are separated (Fig. 75t). The formation of the new dorsal kineties 1, 2, and 3 continues. Caudal cirri differentiate at the posterior end of dorsal kineties 1 and 2. The parental kineties 4 and 5 are completely maintained and form the "new" kinety 4 of the filial products (Fig. 75u, w). After the separation of the proter and the opisthe, the formation of the final cortical pattern

is continued (Fig. 75v). No parental cirri (frontoventral, marginal) are retained after division.

The nuclear apparatus of *P. haideri* divides in the usual way, that is, the macronuclear nodules fuse to a single mass and later divide into the species-specific number of nodules (Fig. 75k–p, r–u, w).

Occurrence and ecology: *Parakahliella haideri* is, like the congeners, probably confined to terrestrial habitats. Type locality is the northern part of Parsch, a district of the city of Salzburg, Austria, where we discovered *P. haideri* in the lower part of a bundle of straw, which was at grassroots level (Berger & Foissner 1989b). The sample was collected on May 2, 1985 by W. Foissner. Since the straw was not primary from the type locality, it cannot be excluded that Salzburg city is not the true type locality (ICZN 1999, Article 76.1.1).

Parakahliella haideri feeds on heterotrophic flagellates and ciliates like peritrichs and *Gonostomum* sp. (Berger & Foissner 1989b). Biomass of 10^6 specimens about 112 mg (Foissner 1998, p. 207).

Afrokahliella gen. nov.

Nomenclature: *Afrokahliella* is a composite of the Latin geographic name *Africa* (the continent) and the genus-group name *Kahliella* (see there for derivation). The name alludes to the fact that the species included occur (mainly) in Africa and were previously assigned to *Parakahliella*. Feminine gender because ending with *-ella* (ICZN 1999, Article 30.1.3).

Characterisation (A = supposed apomorphy): Kahliellidae(?). Adoral zone of membranelles formed like a question mark. Undulating membranes straight and arranged in parallel (A?). Frontal-ventral cirri pattern relatively variable, composed of at least two long or short rows, originates from five anlagen, at least in type species. One or more right and one or more left marginal rows. Transverse cirri lacking. Three bipolar dorsal kineties originating by intrakinetal anlagen, and one dorsomarginal kinety; no parental kineties retained. Caudal cirri at kineties 1 and 2. Terrestrial.

Additional characters: Body very flexible, but acontractile; contractile vacuole at about 50% of body length near left cell margin; dorsal bristles short, that is, around 3 µm long.

Type species: *Parakahliella namibicola* Foissner, Agatha & Berger, 2002a.

Remarks: The three species assigned to *Afrokahliella* (see below) were previously classified in *Parakahliella*. However, they lack the main (sole?) apomorphy of *Parakahliella,* namely the curious preservation of the parental dorsal kineties 4 and 5 as new dorsal kinety 4.[1] The upkeep of this unrewarding situation would make the

[1] Very rarely, one or very few parental(?) bristle(s) occur(s) between dorsal kineties 3 and 4 in *A. halophila* (Fig. 77r). Further, in some populations of this species remnants of parental marginal rows are retained.

characterisation of *Parakahliella* rather woolly. Interestingly, *Parakahliella* and *Afrokahliella* differ not only in this morphological/ontogenetic feature, but also in the geographic distribution: *Parakahliella* is now confined to Europe (probably Eurasia), whereas all three *Afrokahliella* species occur in Namibia. Only *A. halophila* has the type locality in Utah, USA. However, in the original description of this species we already mentioned that the various populations could belong to different (sub)species (Foissner et al. 2002).

The basic cirral and dorsal kinety pattern of the three *Afrokahliella* species is more or less identical, but *A. binucleata* has distinctly more cirri than the other two species and the undulating membranes are somewhat curved and intersecting against straight and arranged in parallel. As already mentioned by Foissner et al. (2002a), the shape of the undulating membranes of *A. binucleata* agrees better with that of *Parakahliella*, than with that of the other two *Afrokahliella* species. But currently I prefer the classification proposed in this review, which upgrades the ontogenesis of the dorsal side and the geography. However, *Afrokahliella binucleata* is classified as incertae sedis to take into account this deviation. *Afrokahliella halophila* has considerably less frontoventral cirri than the type species, but the same undulating membrane pattern. Owing to the high variability, I am unable to perceive an unambiguous apomorphy for *Afrokahliella*. Meaningful molecular data will possibly clear up the situation.

Afrokahliella differs from *Kahliella*, inter alia, by the lack of parental cirral rows, the caudal cirri arrangement (usually two or more cirri on kineties 1 and 2 vs. many on kinety 1), and the oral apparatus (more or less ordinary vs. gonostomatid).

Fragmocirrus Foissner, 2000 is rather similar to *Afrokahliella*, but has transverse cirri, which are admittedly not very prominent and therefore difficult to recognise. Thus, protargol preparations are recommended for a reliable identification. *Afrokahliella binucleata* differs from *F. espeletiae* Foissner, 2000 – the single species of this genus – by the number of macronuclear nodules (two vs. four) and by the distinctly higher number of cirral rows. In *A. namibicola* and *A. halophila* the undulating membranes are arranged in parallel whereas they are curved and optically intersecting in *F. espeletiae*.

Parentocirrus Voss, 1997 also has a similar ventral cirral pattern. However, it has a fragmentation in dorsal kinety 3, strongly indicating (actually proving) that it belongs to the oxytrichids (for review, see Berger 1999, p. 880). By contrast, the lack of such a fragmentation and the presence of a dorsomarginal row in *Afrokahliella* suggest that the new taxon is a non-oxytrichid Dorsomarginalia (Berger 2008).

Bistichella Berger, 2008 lacks a dorsomarginal kinety, indicating that the similarity in the cirral pattern is mainly based on convergent evolution (for review, see Berger 2008, p. 532).

In *Afrokahliella namibicola* the rightmost of the five frontoventral rows is involved in primordia formation (Fig. 76j), indicating that this row is homologous with the row formed from anlage V, because usually (e.g., *Parentocirrus hortualis* Voß, 1997) the cirral row formed by anlage VI does not participate in primordia for-

mation. In hypotrichs with a low number of cirri formed by anlage VI (e.g., 18-cirri hypotrichs), the anterior cirri are the frontoterminals, which are also never involved in anlagen formation. This would mean that cirral row VI is usually lacking in *Afrokahliella*, at least in *A. namibicola*.

Species included in *Afrokahliella* (alphabetically arranged basionyms are given): (1) *Parakahliella namibicola* Foissner, Agatha & Berger, 2002a (type species); (2) *Parakahliella halophila* Foissner, Agatha & Berger, 2002a. Incertae sedis: (3) *Parakahliella binucleata* Foissner, Agatha & Berger, 2002a.

Key to *Afrokahliella* species

If you cannot identify your specimen/population with the key below, see also *Parakahliella* (five dorsal kineties; p. 397), *Fragmocirrus* (transverse cirri present; p. 455), *Bistichella* (only three bipolar dorsal kineties, that is, dorsomarginal kinety lacking; for review, see Berger 2008, p. 532), or *Parentocirrus* (dorsal kinety 3 fragmenting; Berger 1999, p. 878).

1 Two macronuclear nodules (Fig. 76a, i, 79a, f). **2**
- More than two macronuclear nodules[1] (Fig. 77a, n, p, r, t, 78a). . . . . *Afrokahliella halophila* (p. 440)

2 Cortical granules present; undulating membranes long and intersecting; 27–57, on average 39 adoral membranelles (Fig. 79a–k). . . . . *Afrokahliella binucleata* (p. 449)
- Cortical granules lacking; undulating membranes relatively short and in parallel; 21–31, on average 25 adoral membranelles (Fig. 76a–j). . . . . *Afrokahliella namibicola* (p. 434)

Afrokahliella namibicola (Foissner, Agatha & Berger, 2002) comb. nov.

(Fig. 76a–j, Table 23)

2002 ***Parakahliella namibicola* nov. spec.**[2] – Foissner, Agatha & Berger, Denisia, 5: 611, Fig. 138a–j, Table 120 (Fig. 76a–j; original description; the holotype slide [accession number 2002/249] and three paratype slides [2002/250–252] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; see also Aescht 2008, p. 168).

[1] Rarely *A. halophila* also has only two macronuclear nodules.

[2] Foissner et al. (2002a) provided the following diagnosis: Size about 100 × 35 µm in vivo; elongate ellipsoidal. On average 2 macronuclear nodules, 25 adoral membranelles, 1 buccal cirrus, 4 cirri in left frontoventral row, 20 cirri each in middle and right frontoventral row, 5 caudal cirri, and 4 dorsal kineties. 1 right and 1 left marginal row, and 3 frontoventral rows, of which the middle and right extend beyond midbody.

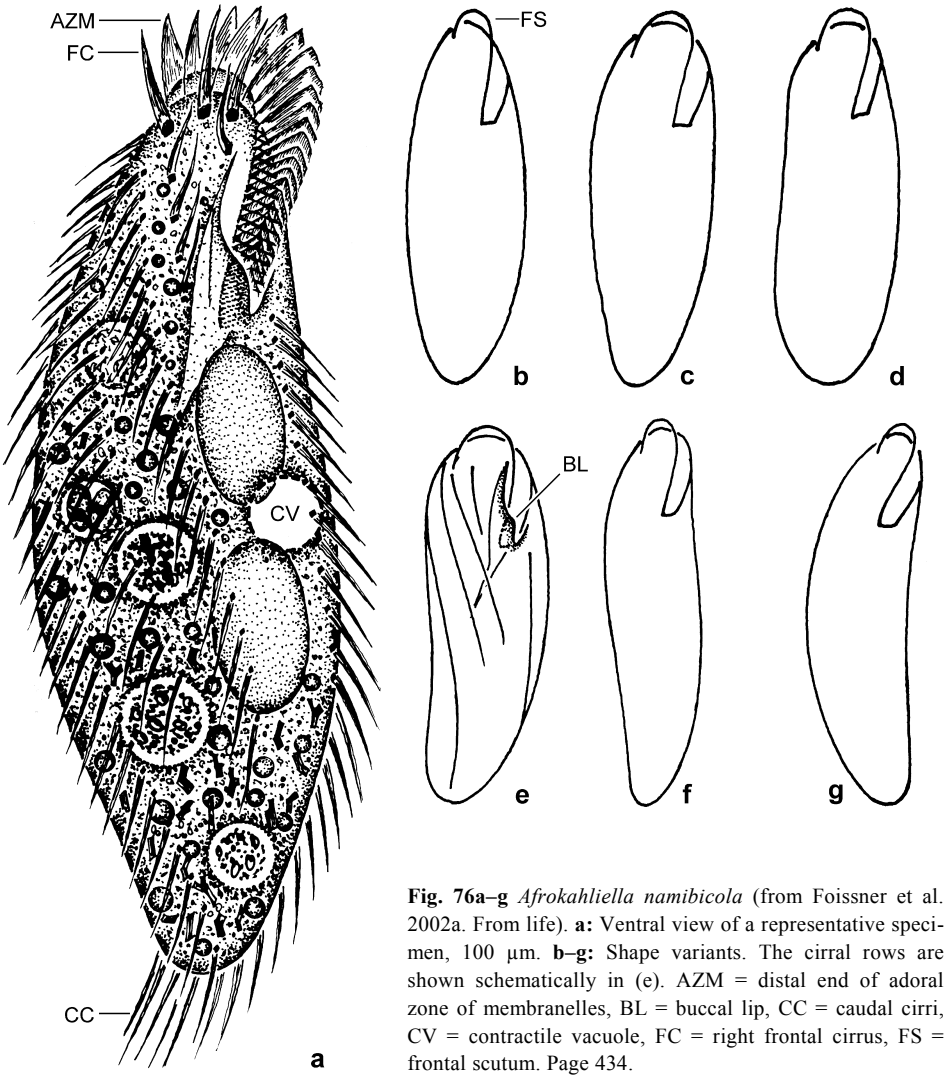


Fig. 76a–g *Afrokahliella namibicola* (from Foissner et al. 2002a. From life). **a:** Ventral view of a representative specimen, 100 µm. **b–g:** Shape variants. The cirral rows are shown schematically in (e). AZM = distal end of adoral zone of membranelles, BL = buccal lip, CC = caudal cirri, CV = contractile vacuole, FC = right frontal cirrus, FS = frontal scutum. Page 434.

Nomenclature: The species-group name *namibicola* (living in the Namib desert) is a composite of *Namib* (the name of the desert), the thematic vowel *-i-*, and the Latin verb *colere* (to live), and refers to the region where the species was discovered (Foissner et al. 2002a). Usually, species-group names ending with *-cola* are considered as appositive substantives and are thus not changed when transferred to a genus of different gender (Werner 1972, p. 138). Type species of *Afrokahliella*.

Remarks: For a foundation of the transfer from *Parakahliella* to *Afrokahliella*, see genus section. *Afrokahliella namibicola* has, like *A. binucleata*, two macronuclear nodules. However, *Afrokahliella binucleata* possesses conspicuous cortical gra-

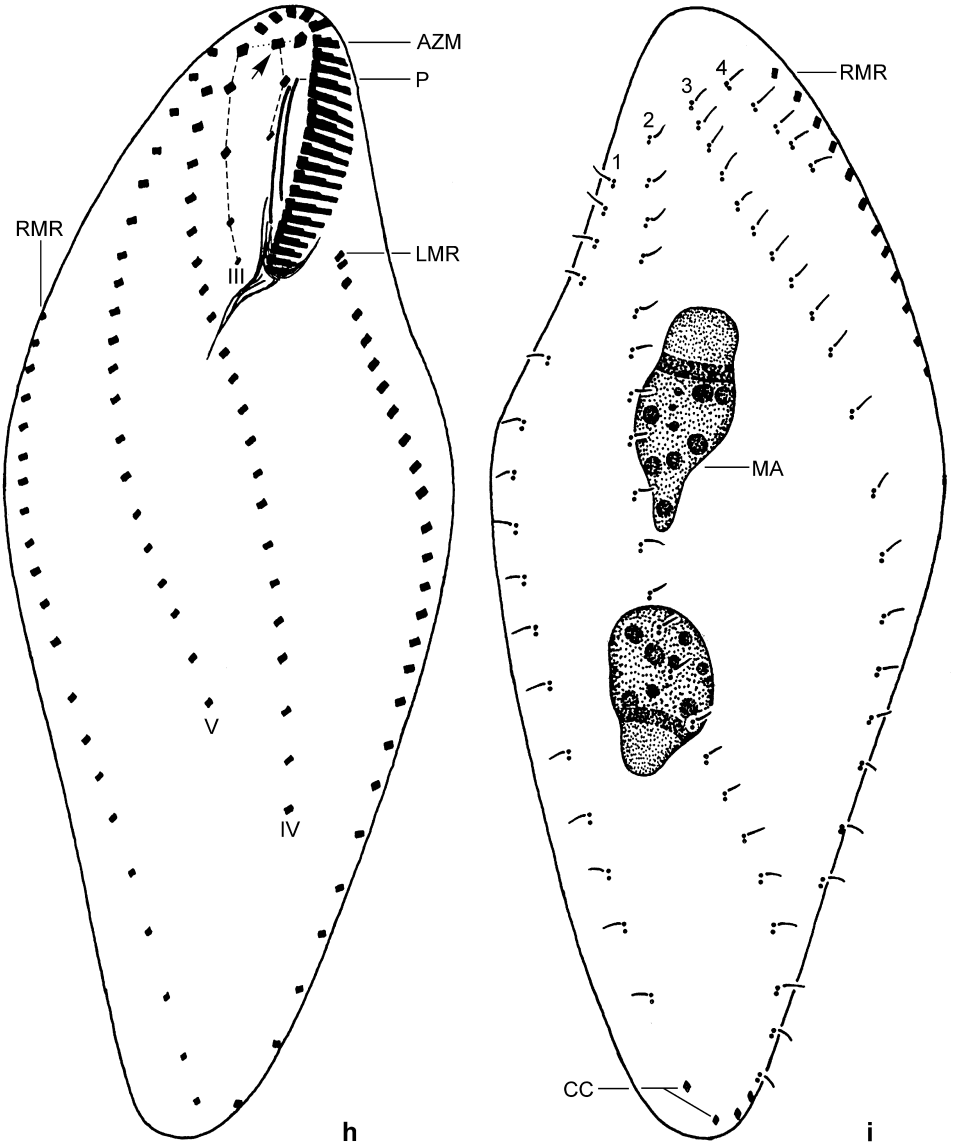


Fig. 76h, i *Afrokahliella namibicola* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 103 µm. Arrow marks middle frontal cirrus, which originates from the same anlage as the buccal cirri (connected by broken line). Doted line connects the three frontal cirri. *Afrokahliella namibicola* invariably has three distinct frontoventral rows (III–V), four dorsal kineties, and is slightly twisted about the main body axis, exposing part of the right marginal row on both ventral and dorsal side. Note the narrow buccal cavity and the straight paroral and endoral extending side by side. This pattern is, together with the simple dorsal kinety pattern (against the preservation of the parental kinety 4 in *Parakahliella*) and the geographic distribution, the main difference to *Parakahliella*. AZM = adoral zone, CC = caudal cirri, LMR = anterior end of left marginal row, MA = anterior macronuclear nodule, P = paroral, RMR = right marginal row, III–V = frontoventral rows (designated as left, middle, and right, respectively, 1–3 in original description), 1–4 = dorsal kineties (kinety 4 is a dorsomarginal row). Page 434.

nules (Fig. 79k), several short and long frontoventral cirral rows, curved and optically intersecting undulating membranes, and distinctly more adoral membranelles. Thus, the present species and *A. binucleata* are easily distinguished, even in life. No other *Afrokahliella* species is twisted about the main body axis. Generally, the cirral pattern of *A. namibicola* is less complicated and variable than that of *A. binucleata* and *Parakahliella* species. The lack of micronuclei is remarkable, but must be confirmed by further studies.

There is a considerable number of similar soil hypotrichs, especially amphisiellids (for review, see Berger 2008), which are easily confused with the present species. See also genus section, for separation from *Fragmocirrus*, *Parentocirrus*, and *Bistichella*. Thus, combined live observation (lack of cortical granules) and silver impregnation is needed for reliable identification. However, if a species has the following combination of features in life, it is likely *Afrokahliella namibicola* (Foissner et al. 2002a): body slightly twisted and about 100 × 35 µm in size, two macronuclear nodules, no cortical granules, two frontoventral rows extending beyond mid-body, several caudal cirri, narrow buccal cavity, and a short (25% of body length) adoral zone composed of about 25 membranelles.

The undulating membranes are arranged side by side and more or less straight (Fig. 76h), which is reminiscent of *Afrokahliella halophila* (see remarks at genus section).

Morphology: Body size 70–120 × 25–45 µm in life, usually near 100 × 35 µm, length:width ratio 1.8–3.9:1, on average 2.7:1 in protargol preparations (Table 23). Body outline highly variable as shown in Fig. 76a–g, basically elongate elliptical with posterior quarter often rather distinctly narrowed and indented at right side, providing cells with a slightly sigmoidal outline. Body very flexible, but acontractile; dorsoventrally flattened up to 2:1, invariably slightly to distinctly twisted about main body axis, marginal cirral rows thus only partially recognisable when specimens are viewed from ventral side (Fig. 76a–g). Nuclear apparatus in middle third of body and, as is usual, left of midline. Number of macronuclear nodules varies from 1–4, but 85% of 113 specimens analysed have two nodules; individual nodules broadly to elongate ellipsoidal, on average near 2:1, outline often irregular, contain many small and some medium-sized chromatin bodies. Micronuclei not unequivocally recognisable in life and protargol preparations, not even in dividers; one micronucleus is possibly present in some specimens. Contractile vacuole at or slightly ahead of mid-body near left body margin, during diastole without distinct collecting canals (Fig. 76a). Cortex colourless and very flexible, without specific granules. Cytoplasm densely granulated providing cells with a brownish shimmer at low magnification (≤ ×100), contains rather many ordinary crystals mainly in posterior third, and food vacuoles up to 15 µm across. Movement inconspicuous, that is, glides slowly on microscope slide and between soil particles.

Adoral zone of ordinary shape and structure, inconspicuous because occupying only 22–32%, on average 27% of body length, composed of an average of 25 membranelles; bases of largest membranelles about 7 µm wide in life (Fig. 76a, h, Table

23). Buccal cavity narrow compared to size of cell and moderately deep; buccal lip rather conspicuous, bears paroral and projects angularly to cover proximal portion of adoral zone. Paroral and endoral almost straight and side by side, paroral commences slightly ahead of endoral and ends a few micrometres ahead of rear end of endoral; paroral cilia tightly spaced, about 7 µm long in life. Pharyngeal fibres inconspicuous both in live and protargol preparations.

Cirral pattern and number of cirri less variable than in other *Afrokahliella* species, that is, of almost ordinary variability (Fig. 76a, h, Table 23). Cirri 10–15 µm long in life, become smaller and more widely spaced in posterior quarter of all rows. Frontal cirri slightly enlarged and close together, form slightly oblique pseudorow. Usually one (rarely two or no) buccal cirrus right of anterior end of paroral, that is, only about 5 µm behind anterior end of cell. Number, length, and arrangement of frontoventral rows rather stable, usually as shown in Fig. 76e. Parabuccal row (formed from anlage III; designated left frontoventral row or frontoventral row 1 in original description) commences behind right frontal cirrus, ends at level of buccal vertex, composed of an average of only four cirri; rarely supernumerary cirri occur left of this row. Left frontoventral row (= middle frontoventral row or frontoventral row 2 in original description) commences at same level as parabuccal row and extends obliquely beyond mid-body, composed of an average of 20 cirri. Right frontoventral row (= right frontoventral row or frontoventral row 3 in original description) begins right of right frontal cirrus, extends obliquely beyond mid-body ending some micrometres ahead of rear end of left frontoventral row, composed of an average of 20 cirri. Transverse cirri lacking. Right marginal row commences dorsally at level of right frontal cirrus and ends, like left row, subterminally. Left marginal row begins left of proximal end of adoral zone; very rarely specimens with a short, second left marginal row occur (Fig. 76h, i).

Dorsal bristles about 3 µm long in life, arranged in four kineties (five in one out of 30 specimens), of which kineties 2 and 3 extend diagonally, mainly due to torsion of body (Fig. 76i). Kineties 1 and 2 distinctly shortened anteriorly, posteriorly associated with an average of three caudal cirri, respectively, one caudal cirrus. Kinety 3 usually distinctly shortened posteriorly, in five out of 23 specimens associated with one or two caudal cirri; kinety 4 (and 5 if present), a dorsomarginal row (see cell division), arranged near anterior right corner of cell, consists of only few bristles (Fig. 76i, Table 23).

Cell division: We found several dividers in the slides from the type location showing basically the same features as in *Parakahliella* (Foissner et al. 2002a). Ontogenesis commences with the formation of an oral primordium close to the postoral portion of the left frontoventral cirral row. Two cirral streaks and a primordium for the undulating membranes are produced by the oral primordium and one streak each by proliferation within the left and right frontoventral rows. Thus, five primordia are recognisable in middle dividers (Fig. 76j); very likely they correspond the anlagen I–V of the ground pattern of the hypotrichs (Berger 2008), that is, anlage VI is (probably) lacking in *A. namibicola* (see remarks at genus section). No transverse

cirri are produced. Caudal cirri are generated at the end of dorsal kineties 1 and 2. Kineties 1–3 divide by intrakinetal proliferation, kinety 4 is a dorsomarginal row.

Occurrence and ecology: Terrestrial. Type locality of *Afrokahliella namibicola* is the Sossus Vlei (24°50´S 15°20´E) in the Southern Namib Desert, where Foissner et al. (2002a) discovered it in the sandy bark from an *Acacia erioloba* (Camel thorn tree; = site 25 in Foissner et al. 2002a). *Afrokahliella namibicola* was almost the only, but very abundant species in this sample in the dunes of the Namib Desert, indicating the highly clumped distribution (Foissner et al. 2002a).

No other *Afrokahliella* species is twisted about the main body axis, indicating that body spiralling might be advantageous in sandy environments. Indeed, *Circinella arenicola* Foissner, 1994a, a very slender, cephalised hypotrich discovered in a dune of North America, is also distinctly spiralised (p. 317). Likewise, *Erimophrya arenicola*, a hypotrich living in the sand dunes of the Namib Desert, is twisted about the main body axis (Foissner et al. 2002a; for review, see Berger 2008, p. 586). We found *A. namibicola* in two other sites (31, 40) of the Namib Desert (Foissner et al. 2002, p. 62), namely in the Central Namib Desert, at a road margin between Welwitschia drive and Bloed-

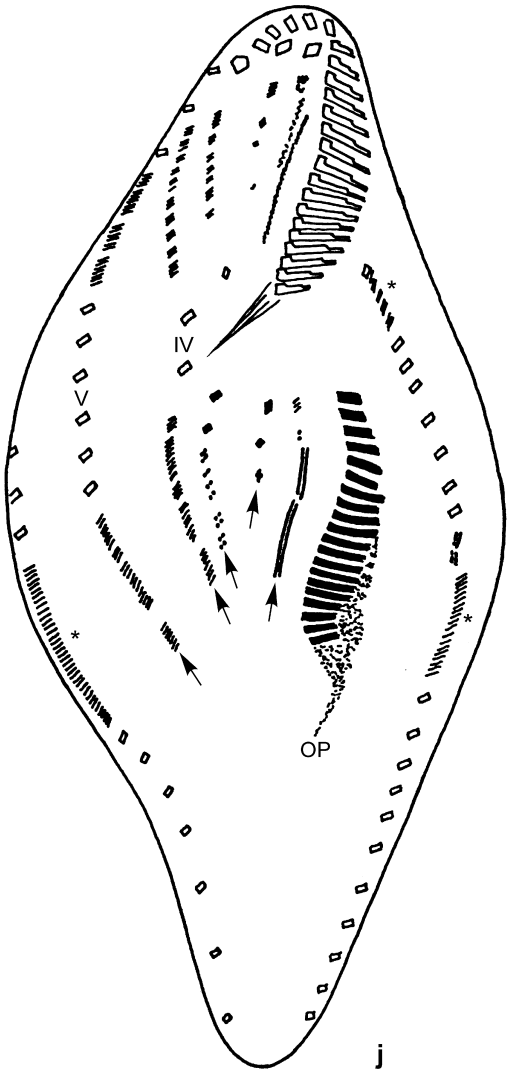


Fig. 76j *Afrokahliella namibicola* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral side of middle divider with macronuclear nodules fused to a single mass (not shown), 72 µm. Parental structures white, new black. Arrows mark the five frontoventral cirral anlagen of the opisthe. The parental cirri between the anlagen IV and V of the proter and opisthe show that the anlagen of the filial products divide independently. Asterisks mark the two anlagen for the left marginal rows, and the anlage of the right marginal row of the opisthe. In the original description, we erroneously designated the anlage for the frontoventral row V of the proter as right marginal row primordium. The parental adoral zone is retained for the proter. OP = oral primordium, IV, V = parental frontoventral rows. Page 434.

koppie (material collected: litter and 0–2 cm soil layer under *Welwitschia* shrubs and decaying blossoms from a succulent shrub), and in the Escarpment of the Central Namib Desert, Spitzkoppe area, about 120 km north-east of the town Swakopmund (material collected: pieces from a decaying *Cyphostemma currorii* tree).

Feeds on naked amoebae and, especially, a *Polytoma*-like flagellate with a size of about 10 × 6 µm and red eye-spot (Foissner et al. 2002a, p. 612; Benin specimens).

Afrokahliella halophila (Foissner, Agatha & Berger, 2002) comb. nov.

(Fig. 77a–t, 78a–l, Table 23)

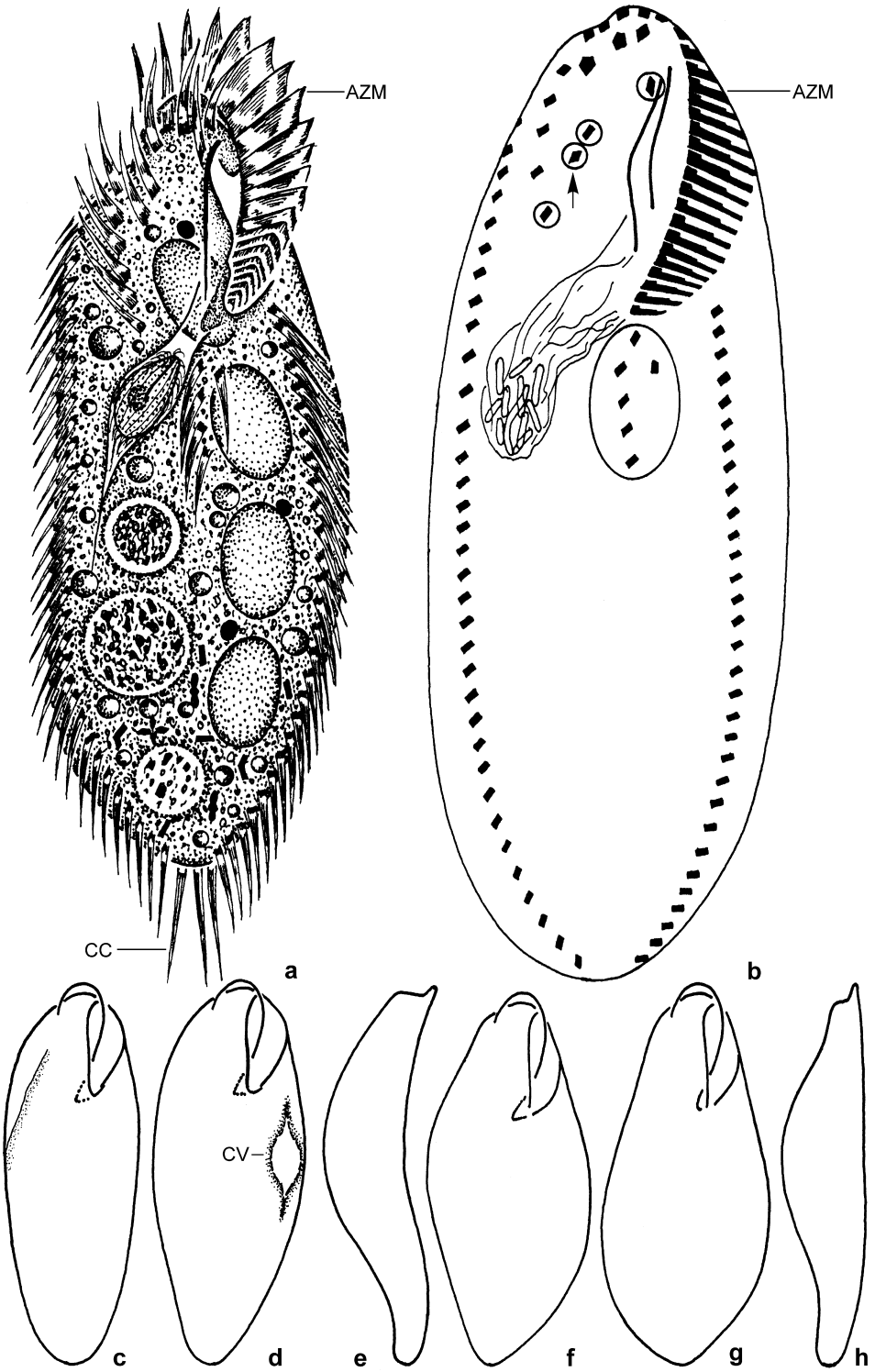
2002 ***Parakahliella halophila* nov. spec.**[1] – Foissner, Agatha & Berger, Denisia, 5: 598, Fig. 136a–u, 384a–l, Table 118 (Fig. 77a–t, 78a–l; original description; the holotype slide [accession number 2002/665], two paratype slides [2002/666, 667], and six voucher slides [2002/668, 669, Namibian site 18; 2002/670–673, Namibian site 59] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; see also Aescht 2008, p. 158).

Nomenclature: The species-group name *halophil·us, -a, -um* (Greek adjective [m; f; n]; salt-loving) is a composite of *halós* (Greek noun; salt) and *philos* (Greek; loving, preferring, friendly) and refers to the saline habitat where the species was discovered (Foissner et al. 2002a).

Remarks: For a foundation of the transfer from *Parakahliella* to *Afrokahliella*, see genus section. Foissner et al. (2002a) studied three populations (ha1, ha3, ha4 in Table 23) of *A. halophila* from two widely separated regions (USA [ha1], Namibia [ha3, ha4]), and the same population (ha1, ha2 in Table 23) two and six days after rewetting the sample. The data showed a high variability between and within the populations, as is evident from a comparison of the specimens two and six days after rewetting. The two-day-specimens from the USA-sample are rather similar to the Namibian site (18) population (Fig. 77m, s), while the six-day-specimens are highly reminiscent of the Namibian site (59) population (Fig. 77o, q). Thus, we did not split

Fig. 77a–h *Afrokahliella halophila* (from Foissner et al. 2002a. a, c–h, from life; b, protargol impregnation). **a:** Ventral view of a representative specimen (104 µm) just ingesting a *Pseudocohnilembus*. **b:** Ventral view of infraciliature (same specimens as in Fig. 77m) with morphogenetically active cirri encircled, 82 µm. In the frontal field of the proter, four cirri produce an anlage each, except for the posterior cirrus (arrow) of the parabuccal row, which produces two anlagen by posterior splitting (see Fig. 77j). **c, d, f, g:** Shape variability. **e, h:** Right lateral views showing dorsoventral flattening. AZM = adoral zone of membranelles, CC = caudal cirri, CV = contractile vacuole. Page 440. →

[1] Foissner et al. (2002) provided the following diagnosis (based on type population only): Size about 90–100 × 35–55 µm in vivo. Ellipsoidal, slightly tapering posteriorly. 4–8, usually 4–5 macronuclear nodules; 18–48, usually 22–27 adoral membranelles; 1 buccal cirrus; 4–13 (usually 5–7) cirri in right frontoventral row and 2–13 (usually 6–9) cirri in left (postoral) frontoventral row; 2–5, usually 3 caudal cirri; and 4 dorsal kineties. 1 right and 1 left marginal cirral row.


AZM
AZM
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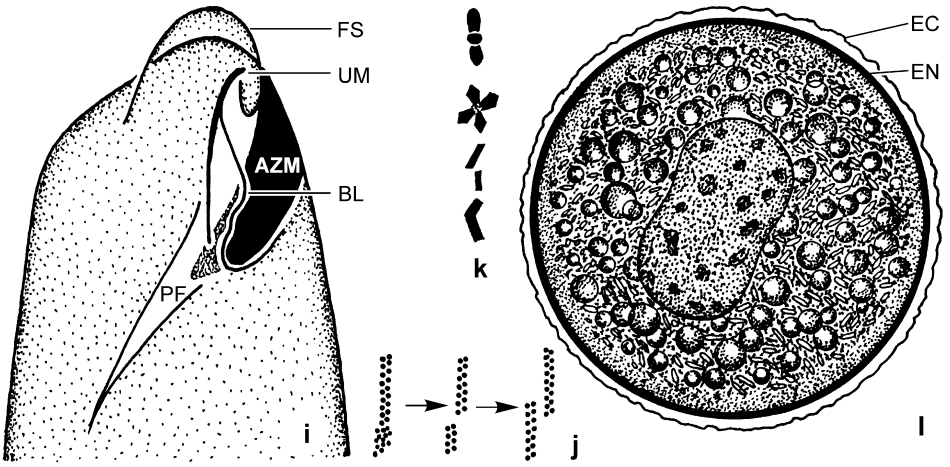


Fig. 77i–l *Afrokahliella halophila* (from Foissner et al. 2002a. i, k, l, from life; j, protargol impregnation). **i:** Oral apparatus. **j:** The posterior parabuccal cirrus (arrow in Fig. 77b) produces two frontal-ventral cirri anlagen for the proter by splitting. **k:** Cytoplasmic crystals. **l:** Resting cyst with dumb-bell-shaped macronucleus. AZM = adoral zone of membranelles, BL = buccal lip, EC = ectocyst, EN = endocyst, FS = frontal scutum, PF = pharyngeal fibres, UM = undulating membranes. Page 440.

Afrokahliella halophila into (sub)species, although molecular methods might show that it is a complex of sibling species (Foissner et al. 2002a).

Parakahliella haideri differs morphometrically rather distinctly from *Afrokahliella halophila*, although the extreme values often overlap (Table 23). The best morphometric feature for distinguishing these species is the number of buccal cirri: *P. haideri* has 1–4, usually three, whereas the present species has 1–2, usually one. A much more important feature are the undulating membranes, which optically cross in *P. haideri* (and *P. macrostoma*, *P. terricola*, and *A. binucleata*; Fig. 73d, 74a, 75d, 79f), while they are invariably side by side in *A. halophila* (Fig. 77b, m, o, q, s, 78a). This conspicuous difference indicates that *A. halophila* and *A. namibicola* could even be not congeneric with *A. binucleata*. This should be proved by meaningful sequence data. *Parakahliella macrostoma*, type of *Parakahliella*, has much more cirri than the present species and has, like *P. haideri*, crossed undulating membranes (see above). In addition, cell division shows that it has two left marginal rows.

Afrokahliella binucleata has more cirri than *A. halophila* and only two macronuclear nodules. Further, it has conspicuous cortical granules (Fig. 79k). *Afrokahliella namibicola* – type of *Afrokahliella* – also has only two macronuclear nodules. *Fragmocirrus espeletiae* Foissner, 2000 also resembles the present species, but has (inconspicuous) transverse cirri and, like *Parakahliella haideri*, usually three buccal cirri.

Morphology: Foissner et al. (2002a) studied three populations (Fig. 77m–t, Table 23). However, we could not exclude that these are different species or subspecies. Thus, we kept the morphometric data separate (Table 23) and diagnosed the

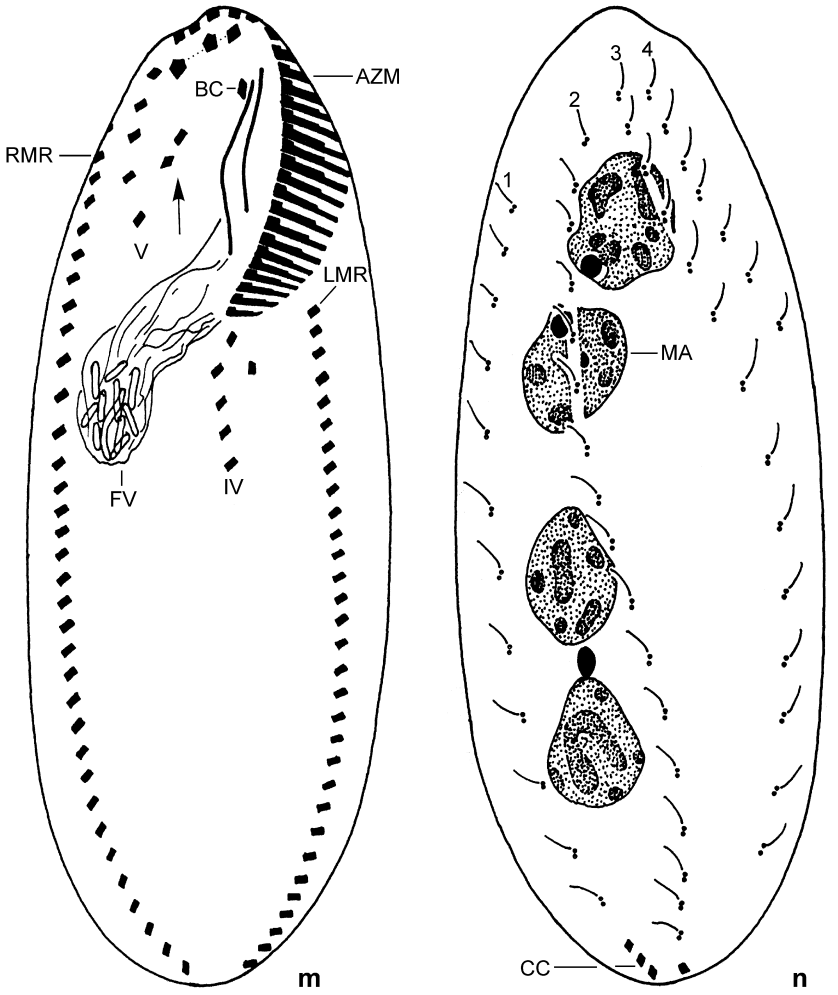


Fig. 77m, n *Afrokahliella halophila* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of a specimen of the type population (USA) two days after rewetting the sample, 82 µm. Arrow marks the cirri left of the right frontoventral row. AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri, FV = descending food vacuole, LMR = left marginal row, MA = macronuclear nodule, RMR = right marginal row, IV = frontoventral row IV (= left frontoventral row), V = frontoventral row V (= right frontoventral row), 1–4 = dorsal kineties (kinety 4 is a dorsomarginal row). Page 440.

species only via the American type population (see footnote at list of synonyms), which, however, embraces the major part of the total variability encountered because some sort of macrostomes developed six days after rewetting the sample (Fig. 77o, Table 23); accordingly, coefficients of variation are unusually high. The "macrostomes" have, on average, slightly more adoral membranelles (27 vs. 22) and macro-

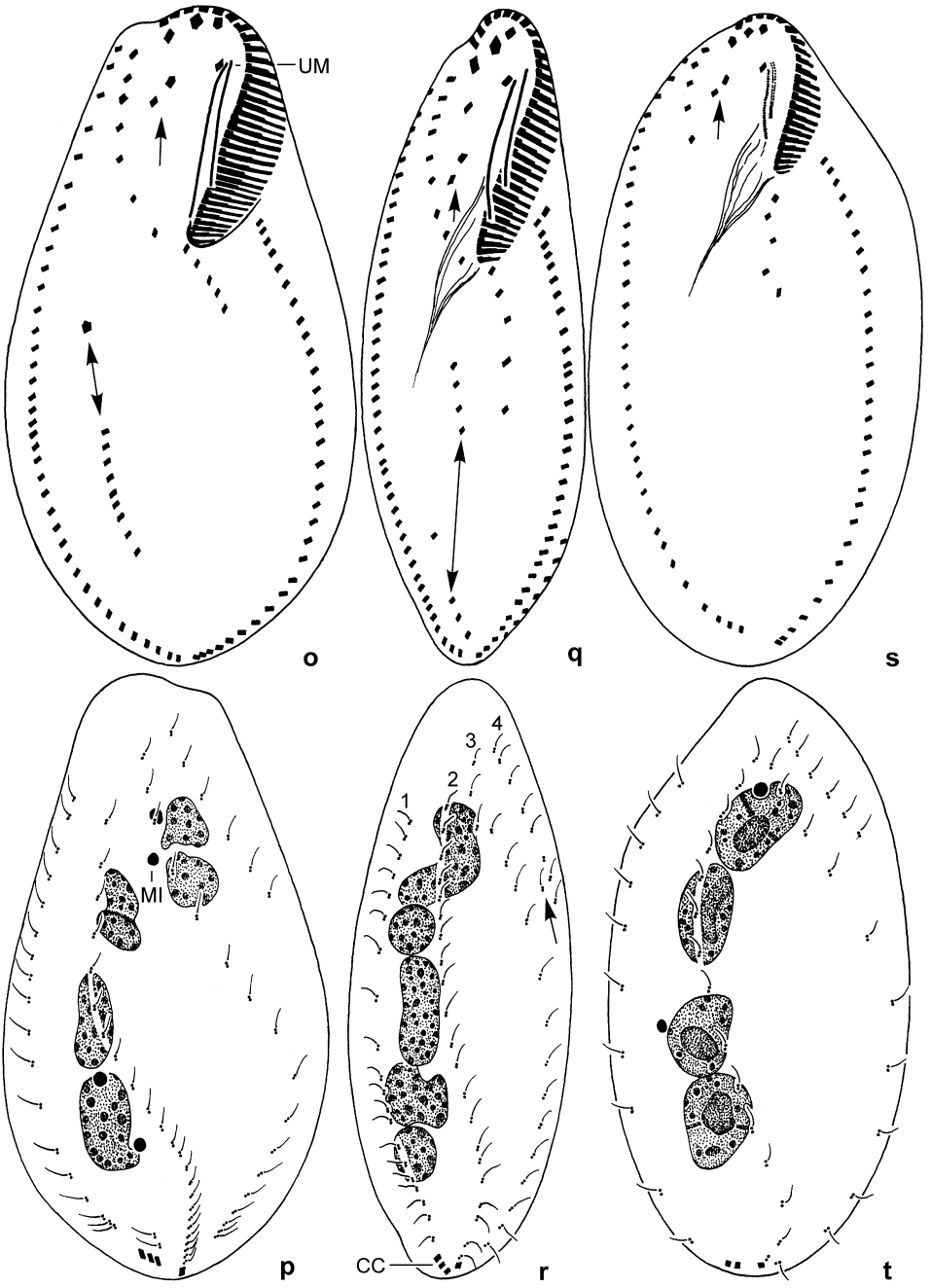


Fig. 77o–t *Afrokahliella halophila* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral (o, q, s) and dorsal (p, r, t) side and nuclear apparatus. Arrows mark cirri left of the right frontoventral row. Note that the undulating membranes have the same pattern in all populations (see also Fig. 77m). Bipolar arrows mark "inner right marginal row". **o, p:** USA type population six days after rewetting the sample, 98 µm. **q, r:** Namibian site (59) population, which is rather similar to the type population six

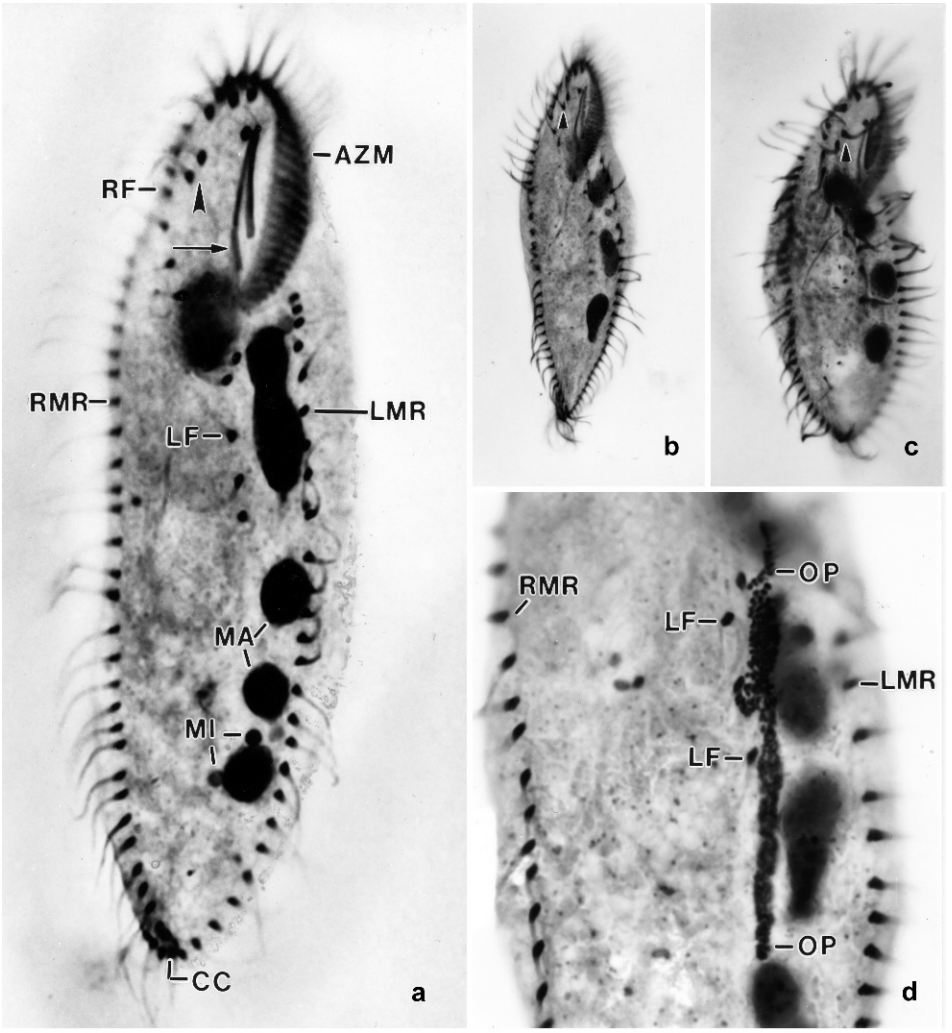


Fig. 78a–d *Afrokahliella halophila* (from Foissner et al. 2002a. Namibian site 59 population after protargol impregnation). **a:** Ventral infraciliature of a representative specimen. Arrow marks posteriorly diverging undulating membranes, an important difference to *Parakahliella* specimens; arrowhead denotes the two cirri of the parabuccal row. **b, c:** Ventral view of a fusiform and an ellipsoidal specimen. Arrowheads mark the two cirri of the parabuccal row. Note the highly variable length:width ratio of the specimens shown in (a–c). **d:** The oral primordium develops postorally along the left frontoventral row, as in *Parakahliella haideri*, whose cell division is very similar to that of the present species. Explanation of original labelling: AZM = adoral zone of membranelles, CC = caudal cirri, LF = left frontoventral row (= frontoventral row IV), LMR = left marginal row, MA = macronuclear nodules, MI = micronuclei, OP = oral primordium, RF = right frontoventral row (= frontoventral row V), RMR = right marginal row. Page 440.

← days after rewetting the sample (o, p), 80 µm. Arrow in (r) marks single (parental?) kinetid forming the "kinety" between kineties 3 and 4. **s, t:** Namibian site (18) population, which is similar to the type population two days after rewetting the sample (m, n), 81 µm. CC = caudal cirri, MI = micronucleus, UM = undulating membranes, 1–4 = dorsal kineties (kinety 4 is a dorsomarginal kinety). Page 440.

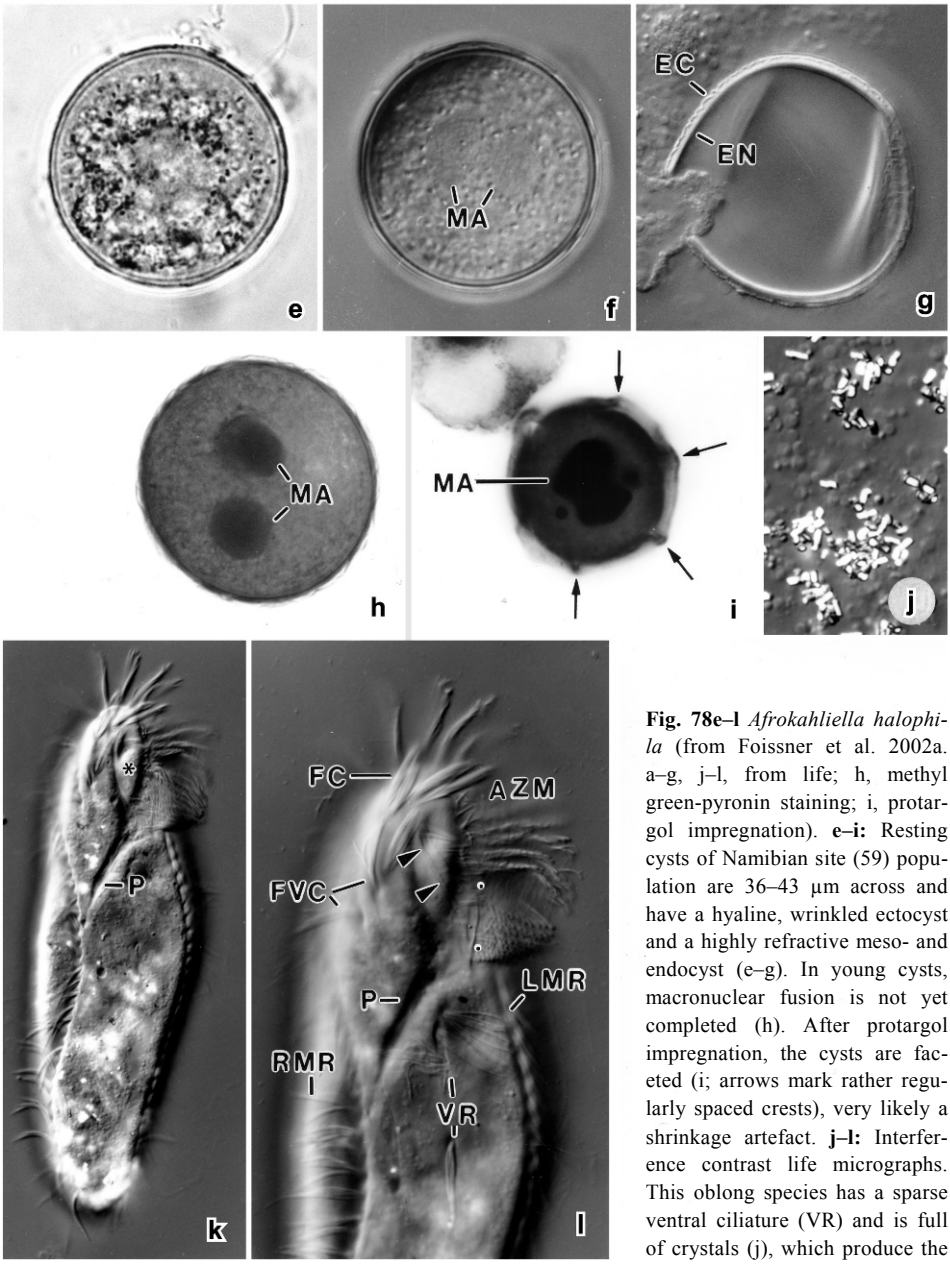


Fig. 78e–l *Afrokahliella halophila* (from Foissner et al. 2002a. a–g, j–l, from life; h, methyl green-pyronin staining; i, protargol impregnation). **e–i:** Resting cysts of Namibian site (59) population are 36–43 µm across and have a hyaline, wrinkled ectocyst and a highly refractive meso- and endocyst (e–g). In young cysts, macronuclear fusion is not yet completed (h). After protargol impregnation, the cysts are faceted (i; arrows mark rather regularly spaced crests), very likely a shrinkage artefact. **j–l:** Interference contrast life micrographs. This oblong species has a sparse ventral ciliature (VR) and is full of crystals (j), which produce the bright spots in figure (k). Arrowheads mark the cleft on the buccal lip containing the proximal end of the paroral cilia; dots denote the left margin of the buccal lip, which covers the narrow, flat buccal cavity (asterisk). Explanation of original labelling: AZM = adoral zone of membranelles, EC= ectocyst, EN = mesocyst and endocyst, FC = frontal cirri, FVC = frontoventral cirri, LMR = left marginal row, MA = macronuclear nodules, P = pharynx, RMR = right marginal row, VR = frontoventral row IV (= left frontoventral row). Page 440.

nuclear nodules (5 vs. 4) than the "normal" cells. In addition, remnants of marginal rows from the previous generation are more frequent.

Body size 80–150 × 30–80 µm in life, usually about 90–100 × 35–55 µm, length:width ratio 1.9–2.4:1 on average in protargol preparations. Body shape also highly variable in all populations, usually ellipsoidal and slightly tapering posteriorly, occasionally fusiform or narrowed tail-like. Body highly flexible, but acontractile; dorsoventrally flattened up to 2:1, ventral side flat or concave, dorsal more or less distinctly vaulted in middle third and with rather conspicuous furrow between kineties 3 and 5 (Fig. 77c, e, f, h, 78a–c, k, l, Table 23). Nuclear apparatus left of midline. Macronuclear nodules in series, usually broadly ellipsoidal (1.6:1 on average), outline often irregular, chromatin bodies small to large. Micronuclei near or attached to macronuclear nodules about 3 µm across in life and thus inconspicuous. Contractile vacuole slightly ahead of mid-body and near left cell margin, with conspicuous collecting canals during diastole. Cortex colourless and very flexible, without specific granules. Cytoplasm with some fat globules 2–4 µm across and few to many colourless crystals concentrated in posterior third of cell (Fig. 78j–l). Food vacuoles 10–20 µm across. Movement without peculiarities, that is, glides rather rapidly on microscope slide and organic debris, showing great flexibility.

Adoral zone inconspicuous because occupying only 25–36%, on average 31% of body length; composed of an average of 22–27 membranelles of ordinary fine structure, bases of largest membranelles about 8 µm wide in life. Buccal cavity narrow, but deep, abuts on adoral zone of membranelles anteriorly, producing fairly characteristic pattern (Fig. 77a, c, d, i). Buccal lip projects angularly to cover mainly posterior half of buccal cavity. Paroral and endoral slightly curved, arranged in parallel, but somewhat diverging posteriorly; both possibly composed of single line of tightly spaced cilia (Fig. 77i, m, o, q, s, 78k, l, Table 23). Pharyngeal fibres of ordinary length and structure.

Cirral pattern and number of cirri highly variable, that is, coefficient of variation often above 10% (Table 23). Cirri about 13 µm long in life, arranged as shown in Fig. 77m, o, q, s, 78a–c, k, l. Pattern somewhat population-specific, but transitions occur, and some specimens of population ha4, which have only three postoral cirri, look similar to an ordinary *Oxytricha* (that is, an 18-cirri hypotrich), except for the lacking transverse cirri. Number of frontoventral cirri low compared to congeners, left of right frontoventral row usually two obliquely arranged cirri (the left one is very like a parabuccal cirrus originating from anlage III; Fig. 77b, m, o, q, s, 78a); invariably one buccal cirrus right of anterior end of paroral. Remnants of parental marginal rows occur only in populations ha2 and ha3 and mainly in posterior half of cell. Lack of transverse cirri confirmed in all populations. Outer right marginal row commences about at level of buccal cirrus, terminates at rear cell end. Left marginal row begins left of proximal part of adoral zone of membranelles, ends very close to rear end of outer right marginal row.

Dorsal bristles about 4 µm long in life, usually arranged in four kineties (Fig. 77n, p, r, t). Kineties 1 and 2 slightly shortened anteriorly, kinety 3 slightly shortened posteriorly; kinety 4, a dorsomarginal row, terminates distinctly ahead of mid-body. Rarely a parental(?) kinety fragment/bristle between kinety 3 and kinety 4 (Fig. 77r).[1] Caudal cirri conspicuous, usually two or three associated with kinety 1, and one cirrus with kinety 2.

Resting cysts: Resting cyst globular, colourless, 36–43 µm across in life (mean = 39.5 µm, SD = 2.3 µm, CV = 5.9%, n = 15; Foissner et al. 2002a). Ectocyst ca. 1 µm thick, hyaline and wrinkled (Fig. 77l, 78e–g). Meso- and endocyst also about 1 µm thick, very compact and thus refractive, smooth; followed by an about 2 µm wide, opaque, finely granulated zone indistinctly separated from main cyst content. Cytoplasm packed with bright fat globules 2–4 µm across and about 1 µm-sized, ellipsoidal inclusions. Macronuclear nodules fused to dumb-bell-shaped or globular mass in ripe cysts (Fig. 77l, 78h, i). Cyst wall up to 4 µm thick and often distinctly faceted in protargol preparations, very likely due to considerable shrinkage (Fig. 78i). Cyst volume is about 26% of vegetative cell volume (Foissner et al. 2006, p. 335).

Cell division: Morphogenesis of cell division was studied by Foissner et al. (2002a). However, since it is very similar to that of *Parakahliella haideri* it was not described in detail. The oral primordium develops along the postoral cirri (Fig. 78d), which are incorporated in the formation of the frontoventral cirri anlagen of the opisthe. Usually six or seven frontoventral cirri primordia each develop in proter and opisthe, including anlage I, which originates, as is usual, from the primordium for the undulating membranes. The posterior cirrus of the cirri left of the right frontoventral row develops two, rarely three anlagen by splitting a primary primordium in the posterior third (Fig. 77b, j). In *P. haideri*, this cirrus generates only one anlage, while the right frontoventral row produces two streaks. Only each one row of right and left marginal cirri is produced, as well as one dorsomarginal kinety (= kinety 4). No transverse cirri are formed. Most parental cirri and dorsal kinetids, which are not involved in anlagen formation, are resorbed. Remnants of the parental marginal cirral rows occur only in populations ha2 and ha3, forming the inner right, respectively, outer left marginal row (Fig. 77o, q, Table 23). Parental dorsal kineties are preserved in populations ha1–3, albeit rarely, forming a row/bristle between kinety 3 and kinety 4 (Fig. 77r), as in *Parakahliella macrostoma* and *P. haideri*.

Occurrence and ecology: Terrestrial. Type locality of *Afrokahliella halophila* is the coast of the Great Salt Lake in Utah, USA, near the town of Birgham (41°30´N 112°W) where Foissner et al. (2002a) discovered it in a highly saline soil sample from a flat, dry puddle. The bottom of the puddle was overgrown with halophytes and covered with a salt crust. The sample contained much litter and plant roots and had pH 8.0. In Namibia, *Afrokahliella halophila* occurred at three sites (18, 59, 61), which are also highly saline. These records indicate that the present species is euryhaline (Foissner et al. 2002a). In the original description we also supposed that *Afro-*

[1] This is reminiscent of the apomorphy of *Parakahliella* (see there).

kahliella halophila has a world-wide distribution (Foissner et al. 2002a). However, one also cannot exclude that it is a group of very similar species, each of which has a restricted distribution.

Afrokahliella halophila is omnivorous, that is, feeds on bacteria, brown fungal conidia, flagellates, ciliates (*Pseudocohnilembus*, *Vorticella astyliformis*, and even small specimens of its own species), and wheat starch (Foissner et al. 2002a).

Incertae sedis

Afrokahliella binucleata (Foissner, Agatha & Berger, 2002) comb. nov.

(Fig. 79a–k, Table 23)

2002 ***Parakahliella binucleata* nov. spec.**[1] – Foissner, Agatha & Berger, Denisia, 5: 607, Fig. 137a–j, 382d, Table 119 (Fig. 79a–k; original description; the "holotype slides" [accession numbers 2002/117, 118] and two paratype slides [2002/119, 120] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria [see nomenclature for problems with holotype]).

Nomenclature: The species-group name *binucleata* (having two nuclei) is a composite of *bi-* (Latin numeral; two) and *nucleát·us, -a, -um* (Latin adjective [m; f; n]; kernel-like), and refers to the two macronuclear nodules, a main feature of the species (Foissner et al. 2002a).

In the original description we fixed two holotype specimens – distributed on two slides – to show both the ventral and dorsal infraciliature clearly (Foissner et al. 2002a, p. 41, 608; Aescht 2008, p. 146). However, this is not possible because only a single specimen can be the holotype (ICZN 1999, Article 73.1.1). According to Aescht (2008) these two specimens, respectively, slides are therefore syntypes (ICZN 1999, Article 73.2), but it cannot be excluded that the situation is more tricky (ICZN 1999, Article 72.3). Both specimens cannot be considered as hapantotype because they do not represent distinct stages in the life cycle of *A. binucleata* (ICZN 1999, Article 73.3, Glossary).

Remarks: For a foundation of the transfer from *Parakahliella* to *Afrokahliella*, see genus section. The infraciliature, for example, the increased number of left marginal rows, the increased number of caudal cirri per dorsal kinety, and the presence of a dorsomarginal kinety as well as and the high variability of the cirral pattern lead us to the classification of the present species in *Parakahliella* (Fig. 79f, h, i, Table 23). However, parental cirri and/or dorsal kineties are obviously lacking so that the present species does not fit the *Parakahliella* diagnoses provided by Berger et al. (1985)

[1] Foissner et al. (2002a) provided the following diagnosis: Size about 140 × 50 µm in vivo; ellipsoidal. 2 macronuclear nodules. Cortical granules in dense rows, colourless, about 1 µm across. 27–57, usually 37 adoral membranelles; 1 or 2, rarely 3 buccal cirri; 3–9, usually 5 frontoventral rows; 2–12, usually 4 caudal cirri on dorsal kinety 1, 1–7, usually 3 on kinety 2, and 1–3, usually 2 on kinety 3; 4 dorsal kineties. 1 right and 1–6, usually 2 left marginal cirral rows.

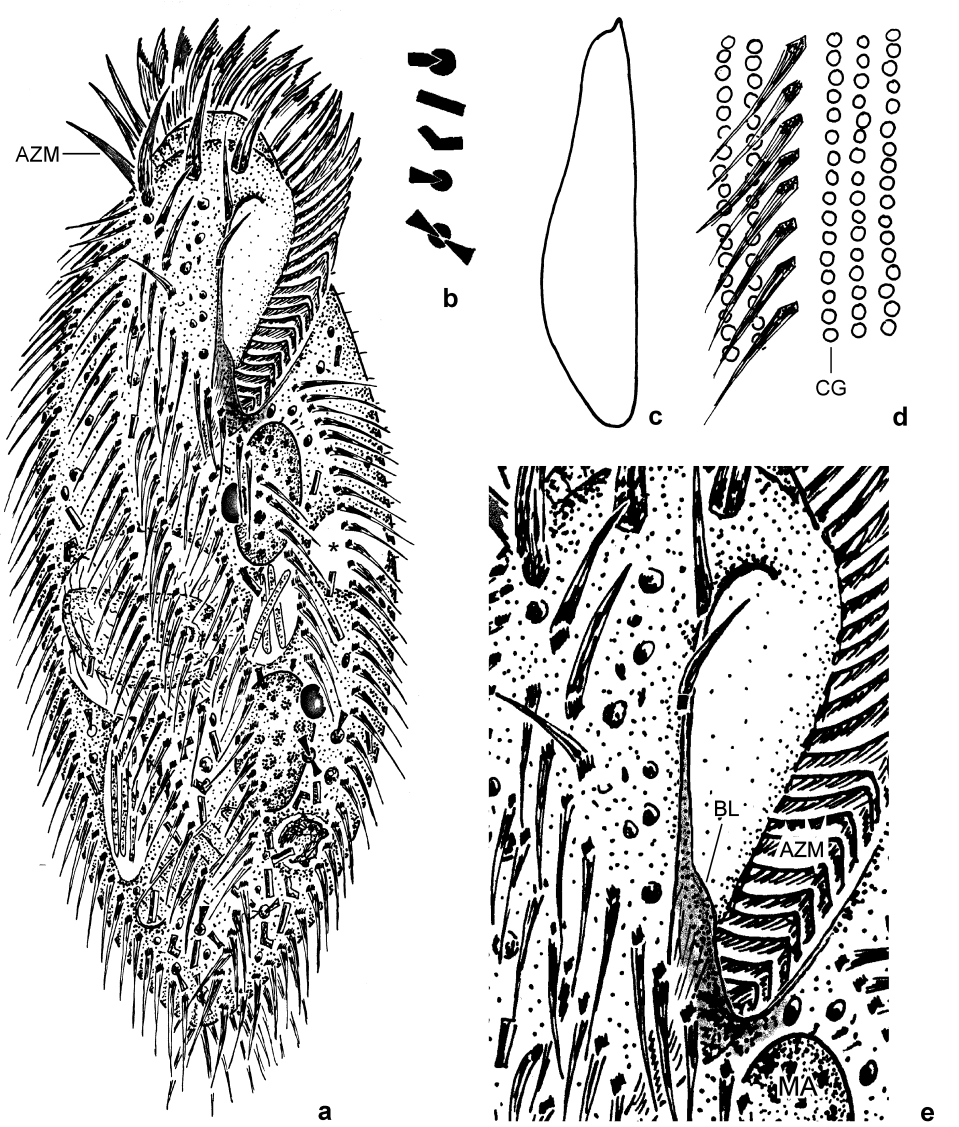


Fig. 79a–e *Afrokahliella binucleata* (from Foissner et al. 2002a. From life). **a:** Ventral view of a representative specimen with an ingested *Colpoda*, 134 µm. **b:** Cytoplasmic crystals are 2–5 µm long. **c:** Right lateral view showing dorsoventral flattening. **d:** The colourless cortical granules are 1.0–1.3 µm across and arranged in closely spaced, meridional rows within which the granules almost abut. **e:** Oral area showing inconspicuous buccal lip. AZM = adoral zone of membranelles, BL = buccal lip, CG = cortical granules, MA = macronuclear nodule. Page 449.

and Berger & Foissner (1989b) very well (see footnotes at genus section). Thus, it is classified, together with two other "*Parakahliella*"-species, in *Afrokahliella*.

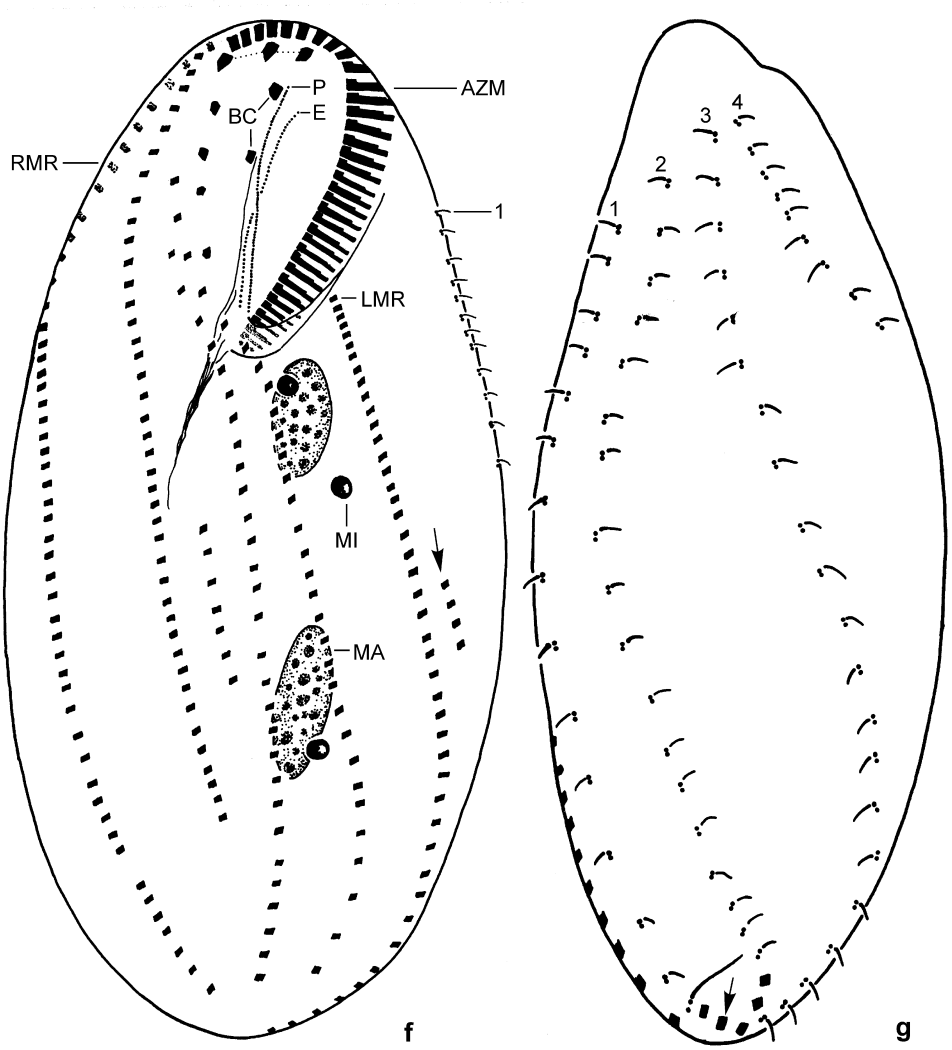
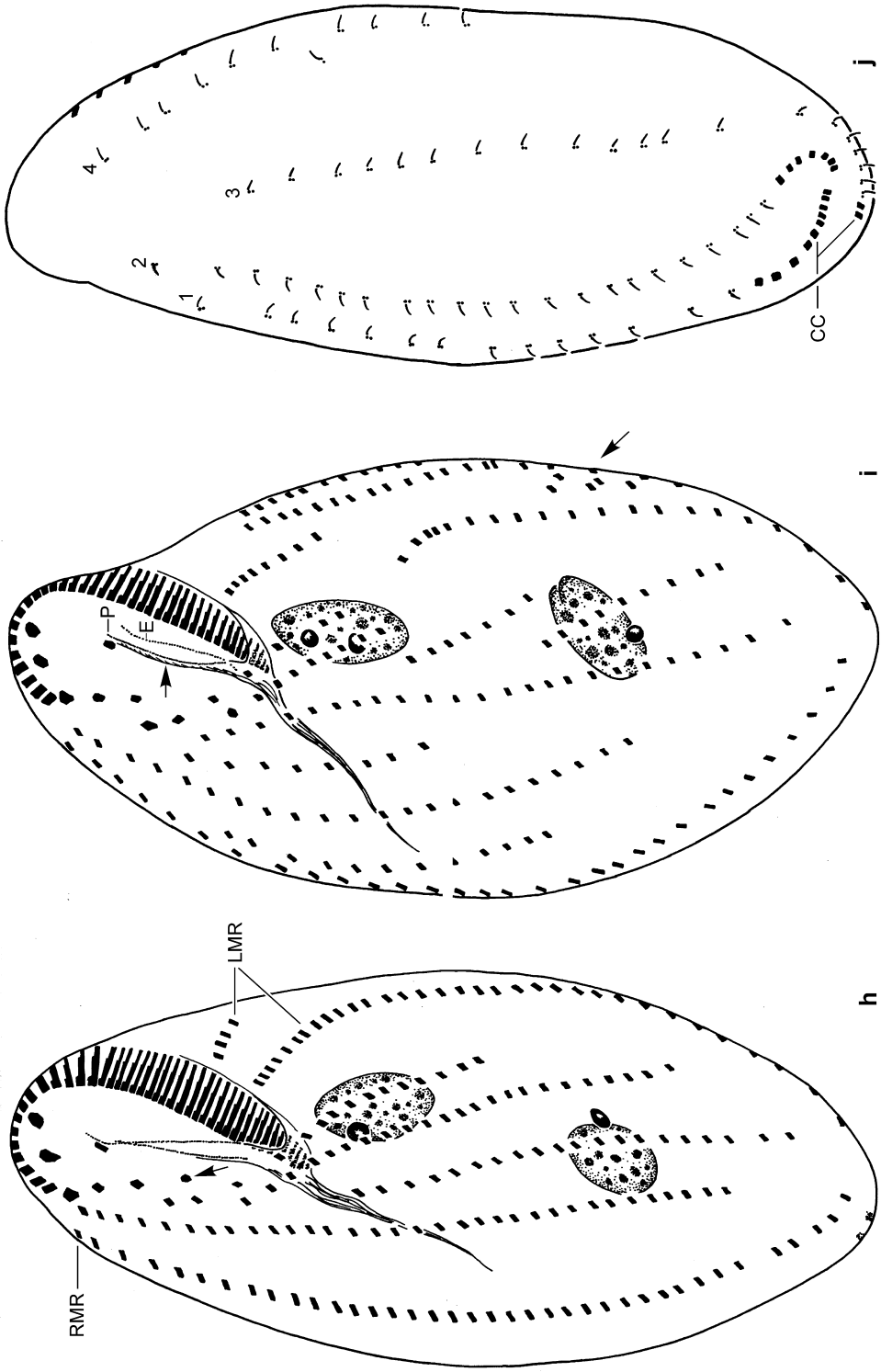


Fig. 79f, g *Afrokahliella binucleata* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of two specimens which were incorrectly designated as holotype specimens in the original description (see nomenclature), f = 160 µm, g = 120 µm. Dotted line in (f) connects frontal cirri. Arrow in (f) marks a short left marginal row, arrow in (g) denotes a caudal cirrus. AZM = adoral zone of membranelles, BC = buccal cirri, E = endoral, P = paroral, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row, 1–4 = dorsal kineties (kinety 4 is a dorsomarginal kinety). Page 449.

Afrokahliella binucleata is the sole species with caudal cirri on dorsal kinety 3 and with cortical granules, and only *A. namibicola* (type species) also has two macronuclear nodules. However, *Afrokahliella namibicola* has a rather simple cirral pattern and its body is slightly twisted about the main body axis. Thus, these two spe-


h
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cies can be easily separated even in life. *Paraurostyla weissei* (Stein, 1859) Borror, 1972 and *Paraurostyla granulifera* Berger & Foissner, 1989a, which have a very similar general appearance, have transverse cirri and a fragmenting dorsal kinety (fragmentation not confirmed for *P. granulifera*), showing that they (at least *P. weissei*) belong to the oxytrichids (for review, see Berger 1999, p. 844, 874).

Morphology: Body size 120–190 × 35–65 µm in life, usually near 140 × 50 µm, length:width ratio about 2.6–3.6:1 in life and 1.7–3.3:1 (2.2:1 on average; Table 23) in protargol preparations, where specimens tend to become inflated. Body very flexible, but acontractile. Body outline elliptical to slightly fusiform (Fig. 79a); dorsoventrally flattened up to 1.5:1, ventral side flat, dorsal distinctly vaulted in posterior half (Fig. 79c). Macronuclear nodules in middle third of cell slightly left of midline, ellipsoidal to elongate ellipsoidal, with numerous globular chromatin bodies 1–2 µm across; rather small compared to size of cell (Fig. 79a, f, h, i). Micronuclei usually attached or near macronuclear nodules, globular, about 5 × 4 µm in life. Contractile vacuole in mid-body at left cell margin. Cortical granules in closely spaced meridional rows (Fig. 79d, k); individual granules inconspicuous because only 1.0–1.3 µm across and colourless, have a central, dark dot (cavity?) so that they look like glass beads (Fig. 79k); impregnate more or less intensely with protargol and become bright red, but not released when methyl green-pyronin is added. Cytoplasm colourless, with many small crystals concentrated in posterior third of cell. Food vacuoles up to 30 µm in diameter. Movement without peculiarities, that is, glides moderately quickly on microscope slide and debris showing great flexibility.

Adoral zone occupies 21–40%, on average 31% of body length, composed of an average of 37 membranelles, bases of largest membranelles about 7 µm wide in life. Buccal cavity narrow and flat (Fig. 79a, e, f). Buccal lip inconspicuous, covers only proximal portion of adoral zone. Paroral and endoral usually slightly curved and optically crossed in mid-portion (Fig. 79f); exact arrangement of membranes, however, difficult to recognise in many specimens; both likely composed of a single line of tightly spaced cilia; paroral cilia about 7 µm long in life. Pharyngeal fibres of ordinary length and structure.

Cirral pattern and number of cirri highly variable, as in (the closely related genus?) *Parakahliella* (Fig. 79f, h, i, Table 23). Frontal cirri distinctly, cirri behind right frontal cirrus slightly enlarged. One buccal cirrus right of anterior end of paroral; in about 50% of specimens a second, rarely a third buccal cirrus occurs at midregion of paroral. Number, length, and arrangement of frontoventral rows highly variable, that is, none of the patterns can be considered as "representative" (Fig. 79f, h, i). Transverse cirri lacking. Right marginal row commences at level of right fron-

← **Fig. 79h–j** *Afrokahliella binucleata* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus, h = 114 µm, i = 123 µm, j = 51 µm. Arrow in (h) marks the short cirral row (= parabuccal cirri) behind the right frontal cirrus. Oblique arrow in (i) denotes the region with widely spaced marginal cirri, likely remnants of parental rows. Horizontal arrow in (i) marks line formed by pharyngeal fibres. CC = caudal cirri, E = endoral, LMR = left marginal rows, P = paroral, RMR = right marginal row, 1–4 = dorsal kineties (kinety 4 is a dorsomarginal row). Page 449.

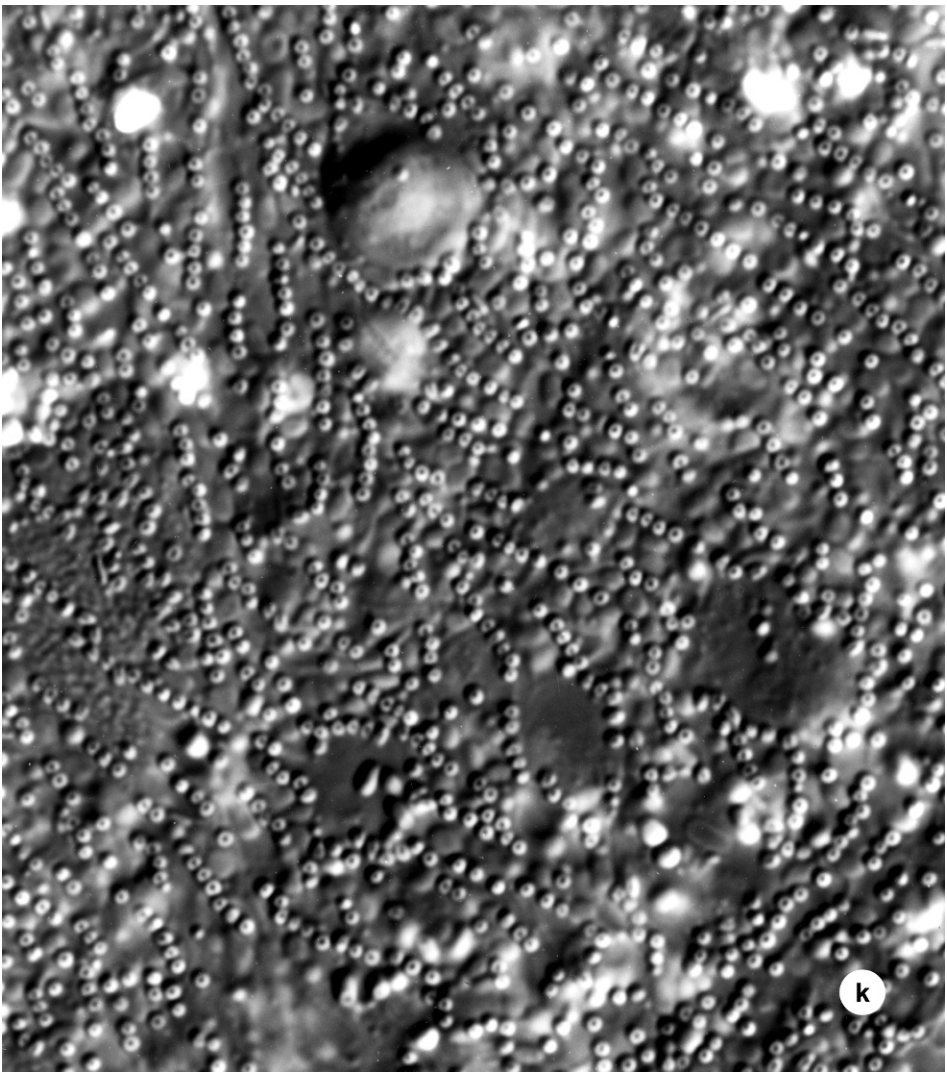

Fig. 79k *Afrokahliella binucleata* (from Foissner et al. 2002a. Specimens from Namibian site [50] from life, interference contrast). The cortical granules are arranged in closely spaced, meridional rows, somewhat disorganised in this squeezed cell. The individual granules are 1.0–1.3 µm across, colourless, and have a central, dark dot (cavity?) so that they look like glass beads. Page 449.

tal cirrus and ends subterminally. Left marginal ciliature variable, that is, usually one long row commences left of proximal portion of adoral zone and terminates at rear end of cell, plus one or two short to long rows at variable positions left of long row. Some specimens with more than three left marginal rows of rather different length, arrangement, and distances between cirri; possibly they are residues of left

marginal rows of previous generations (Fig. 79f, h, i). Frontoventral and marginal cirri about 12–15 µm long in life.

Dorsal bristles about 3 µm long in life, arranged in four rows. Kinety 1 usually slightly more shortened anteriorly than remaining kineties. Kineties 1–3 extend to rear cell end, each of them with caudal cirri (Fig. 79g, j, Table 23). Kinety 4, a dorsomarginal row, terminates about at level of buccal vertex. Dorsal ciliary pattern often difficult to recognise due to cortical granulation. Caudal cirri, although present in considerable number (6–18), inconspicuous in life because of similar size as marginal cirri (Table 23).

Cell division: We found one late divider showing that the dorsal kineties 1–3 do not fragment, and one dorsomarginal kinety (= kinety 4) is formed (Foissner et al. 2002a, p. 610). Since in total only four kineties are present (Table 23), no parental kinety is obviously retained.

Occurrence and ecology: Terrestrial. Type locality of *A. binucleata* is the Aus water-hole (19°10´S 16°10´E; site 64 in Foissner et al. 2002a), Etosha National Park, Namibia, where it was discovered in a soil sample from a water-hole which was dry and overgrown with grasses and some sedges. The sample was composed of litter, roots, and soil from 0–5 cm in the central area of the water-hole (pH 6.3, slightly saline [0.05%]). In addition, we found it in litter and soil from an alluvial grassland within the *Colophospermum mopane* forest surrounding the Bambatsi Guest Farm between the towns Khorixas and Outju, Namibia (site 50 in Foissner et al. 2002a). No further records published.

Afrokahliella binucleata is omnivorous, that is, feeds on long bacterial rods, filamentous cyanobacteria, *Polytomella*, amoebas, and ciliates, like small *Colpoda* species (Foissner et al. 2002a).

Fragmocirrus Foissner, 2000

2000 ***Fragmocirrus* nov. gen.**[1] – Foissner, Stud. Neotrop. Fauna & Environm., 35: 61 (original description). Type species (by original designation): *Fragmocirrus espeletiae* Foissner, 2000.
2001 ***Fragmocirrus* Foissner 2000** – Aescht, Denisia, 1: 73 (catalogue of generic names of ciliates).
2001 ***Fragmocirrus* Foissner, 2000** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 28 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2007 ***Fragmocirrus* Foissner, 2000** – Jankowski, Ciliophora, p. 462 (revision of ciliates).
2008 ***Fragmocirrus* Foissner, 2000** – Lynn, Ciliated protozoa, p. 357 (revision of ciliates).

Nomenclature: *Fragmocirrus* is a composite of the Latin noun *fragmentum* (fragment), the thematic vowel ·*o*-, and the Latin noun *cirrus* (curl; compound cilia typical for hypotrichs), meaning a hypotrichous ciliate with fragmented or incomplete ventral cirral rows. Masculine gender (Foissner 2000).

[1] Foissner (2000) provided the following diagnosis: Parakahliellidae Eigner, 1997 with transverse and caudal cirri. Ventral cirral rows 4 and 5 each develop a V-shaped anlage producing proter's and opisthe's cirral rows 4 and 5. Two or more rows each of right and left marginal cirri, inner right and outer left row(s) more or less distinctly reduced. Dorsal kineties generated by within anlagen and dorsomarginally.

Characterisation (A = supposed apomorphy): Kahliellidae(?). Adoral zone of membranelles formed like a question mark. Undulating membranes long, curved, and optically intersecting. Frontoventral cirri pattern composed of three frontal cirri, a buccal row, a parabuccal row, and two more or less long frontoventral rows. Transverse cirri present. One or more left and one or more right marginal rows, inner right and outer left rows more or less distinctly reduced. Three bipolar dorsal kineties originating by intrakinetal proliferation, and one dorsomarginal kinety. Caudal cirri on dorsal kineties 1 and 2. Dorsal kinety fragmentation lacking. No parental cirri or dorsal bristles retained in postdividers. Terrestrial.

Remarks: For details, see type species. Kamra et al. (2008, p. 375) recorded a *Fragmocirrus* sp. from a soil sample from the Valley of Flowers, Nanda Devi Biosphere Reserve, India; no details have been provided.

Species included in *Fragmocirrus*: (1) *Fragmocirrus espeletiae* Foissner, 2000.

Single species

Fragmocirrus espeletiae Foissner, 2000
(Fig. 80a–h, Table 24)

2000 ***Fragmocirrus espeletiae* nov. spec.**[1] – Foissner, Stud. Neotrop. Fauna & Environm., 35: 64, Fig. 42–83, Table 3 (Fig. 80a–h; original description; one holotype slide [accession number 2000/118] and five paratype slides [2000/119–123] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Aescht 2008, p. 153).

2001 ***Fragmocirrus espeletiae* Foissner, 2000** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 28 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: The species-group name *espeletiae* is the genitive of the genus-group name *Espeletia*, the plant on which the species was found (Foissner 2000).

Remarks: Foissner (2000) classified *Fragmocirrus* in the Parakahliellidae obviously because of the V-shaped cirral primordia producing the left and right frontoventral rows. He compared it with *Paraurostyla*, *Parakahliella*, and *Parentocirrus* (Foissner 2000, p. 65). However, as explained in the remarks of the Kahliellidae, I suppose that only *Parakahliella* is more or less closely related to *Fragmocirrus* as indicated by the ventral cirral pattern and its formation during cell division, and especially by agreements in the dorsal kinety formation, basically the lack of a kinety fragmentation and the presence of a dorsomarginal kinety. By contrast, *Paraurostyla*

[1] Foissner (2000) provided the following diagnosis: Size in vivo about 160 × 60 µm; ellipsoidal. Four macronuclear nodules, 2 micronuclei, 36 adoral membranelles, 3 frontal cirri, 3 buccal cirri, 3 transverse cirri, and 3 caudal cirri on average. Five ventral cirral rows (anlagen) composed of 1 (1st frontal cirrus), 4 (2nd frontal cirrus plus buccal cirri), 4 (3rd frontal cirrus plus cirri underneath), 18 (row 4), and 14 (row 5) cirri on average. Four dorsal kineties, rows 1–3 originate intrakinetally, row 4 originates dorsomarginally and terminates near mid-body; rows 1 and 2 produce caudal cirri.

and *Parentocirrus* have an oxytrichid kinety fragmentation (the rear portion of the anlage of kinety 3 forms kinety 4) showing that they are oxytrichids.

Jankowski (2007) and Lynn (2008) classify *Fragmocirrus* as incertae sedis in the Kahliellidae. As explained in the kahliellid section, I consider this group only as melting pot for hypotrichs with usually one or two more or less long frontoventral rows and with usually three bipolar dorsal kineties and usually one dorsomarginal kinety. One characteristic feature of the name-bearing type genus *Kahliella* is lacking in *Fragmocirrus*, namely the preservation of parental cirri. Perhaps relevant molecular data will improve our knowledge of the phylogenetic position of this species, which is perhaps confined to the (south) American continent.

Morphology: Like other members of the kahliellids, *Fragmocirrus espeletiae* has a rather variable cirral pattern and number of macronuclear nodules.

Body size in life 130–280 × 40–100 µm, usually about 160 × 60 µm; length to width ratio only slightly variable, that is, 2–3:1, with an average of 2.6:1 (Table 24). Body very flexible, but acontractile. Body outline elliptical to fusiform, occasionally slightly narrowed posteriorly, anterior end rather broadly rounded, posterior end narrowly rounded to bluntly pointed (Fig. 80a–c). Body dorsoventrally flattened up to 2:1 (Fig. 80d). Usually four macronuclear nodules, arranged in line left of cell's midline; individual nodules broadly to slenderly ellipsoidal, near or attached to macronuclear nodules in variable positions (Fig. 80a, g). Contractile vacuole slightly ahead of mid-body at left cell margin, during diastole with two short, lacunar collecting canals (Fig. 80a, b). Specific cortical granules lacking; however, there are many 2–4 × 1–2 µm-sized crystals, which very likely originate from rings of bright granules near the cortex and in the cytoplasm (Fig. 80e). Cytoplasm colourless, but cells appear dark at low (≤100×) magnification when packed with crystals as described above, some fat globules up to 15 µm across, and up to 40 µm-sized food vacuoles. Movement without peculiarities, that is, glides moderately fast on substrate and never rests.

Adoral zone occupies 35% of body length on average, composed of 37 membranelles of usual fine structure (Fig. 80a, f, Table 24). Buccal cavity deep, but rather narrow, anterior portion semicircularly curved in life; buccal lip long and rather broad, masking right half of buccal cavity (Fig. 80a–c, f). Paroral slightly curved, optically intersecting with endoral about at level of rearmost two buccal cirri; both membranes very likely composed of narrowly spaced dikinetids; pharyngeal fibres distinct (Fig. 80f).

Cirral pattern rather variable mainly due to the marginal ciliature and a varying number of frontal-ventral-transverse cirri anlagen (see below; Fig. 80a, f). Three enlarged frontal cirri form slightly curved pseudorow. Usually three buccal cirri right of anterior half of paroral, bases become smaller from anterior to posterior.[1] On average three parabuccal cirri behind right frontal cirrus. Left frontoventral row commences right of buccal vertex, terminates distinctly ahead of transverse cirri, for ex-

[1] In the original description (Foissner 2000) cirral rows are designated with 1 (left frontal cirrus) to 5 (right frontoventral row).

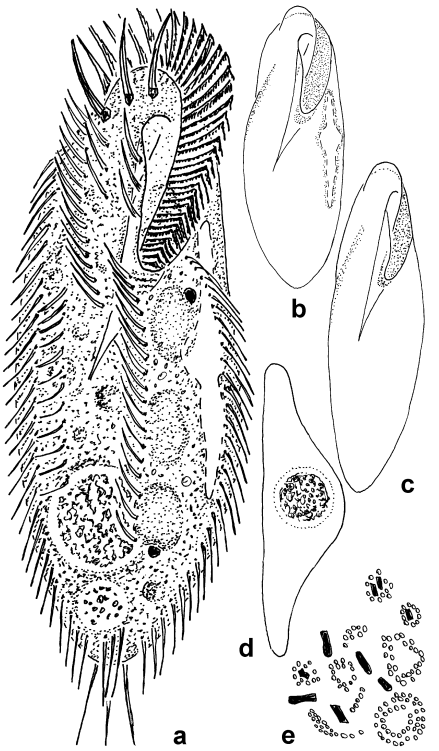

Fig. 80a–e *Fragmocirrus espeletiae* (after Foissner 2000. From life). **a:** Ventral view of a representative specimen, 170 µm. **b, c:** Shape variants showing, inter alia, contractile vacuole with collecting canals (b). **d:** Right lateral view of a specimen with a large food vacuole. **e:** Crystals near cortex and in cytoplasm. Crystals probably originate within ring-shaped arrays of bright granules. Page 456.

ample, at 78% of body length in specimen illustrated (Fig. 80f). Right frontoventral row begins right of right frontal cirrus and terminates about at level of buccal vertex right of cell midline, usually more or less distinctly overlapping with left frontoventral row; terminates at 36% of body length in specimen illustrated (Fig. 80f). Usually three triangularly arranged pretransverse ventral and transverse cirri in gap between rear end of marginal rows, project distinctly beyond rear cell margin; very likely one transverse cirrus originates from anlage forming left frontoventral row, whereas one pretransverse ventral cirrus and one transverse cirrus are formed from anlage producing right frontoventral row (exact decision not possibly because relevant divider not shown). Marginal ciliature rather variable, usually composed of a long outer right row somewhat shortened anteriorly and terminating about at level of transverse cirri; inner left marginal row begins left of proximal portion of adoral zone, extends to very near cell end. Marginal ciliature rather variable because both inner right row(s) and outer left row(s) (i) more or less distinctly reduced, (ii) complete, or (iii) even lacking.

Dorsal bristles in life about 3 µm long, invariable arranged in four kineties; kinety 1 extends – like row 2 – left of cell's midline, both more or less distinctly shortened anteriorly. Kinety 3 runs right of midline, slightly shortened anteriorly and posteriorly. Kinety 4, a dorsomarginal kinety, in distinct furrow near right margin of cell, terminates at about 50% of body length (Fig. 80g). No parental basal bodies present after division. Caudal cirri conspicuous because 20 µm long and rather motile; usually two, rarely three cirri on kinety 1 and usually one, rarely two cirri on kinety 2. Interestingly, bristles originate from the rear basal body (misobservation?) according to Fig. 80g, whereas they are attached to the anterior basal body in all(?) other hypotrichs (for figures see Berger 1999, 2006, 2008). I suppose that this is a misobservation.

Cell division: Foissner (2000) studied this part of the life cycle in detail. Accordingly, it is very similar to that of *Parakahliella macrostoma* and *P. haideri* (p.

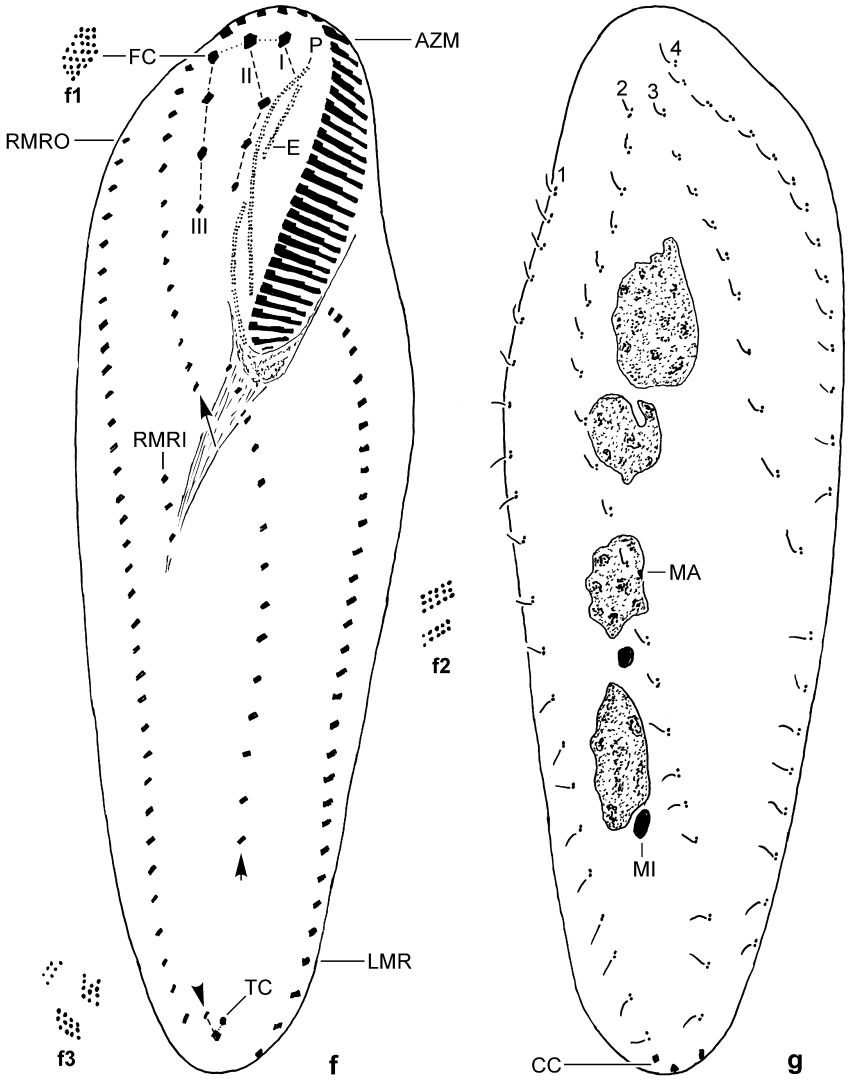

Fig. 80f, g *Fragmocirrus espeletiae* (after Foissner 2000. Protargol impregnation). **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 163 µm. Short arrow marks rear end of left, long arrow marks rear end of right frontoventral row. *Fragmocirrus espeletiae* usually has one pretransverse ventral cirrus (arrowhead) and two transverse cirri forming a V-shaped pattern. Cirri originating from same anlage connected by broken line (only shown for anlagen I–III). Frontal cirri connected by dotted line. **f1–f3:** Right frontal cirrus (f1), left marginal cirri (f2), and pretransverse ventral and transverse cirri (f3). AZM = adoral zone of membranelles, CC = caudal cirri (usually two on kinety 1 and one on kinety 2), E = endoral, FC = right frontal cirrus, MA = macronuclear nodule, MI = micronucleus, LMR = left marginal row, P = paroral, RMRI = inner right marginal row, RMRO = outer right marginal row, TC = transverse cirri (arrowhead likely marks pretransverse ventral cirrus), I–III = frontal-ventral-transverse cirri anlagen/rows, 1–4 = dorsal kineties (kinety 4 is a dorsomarginal row). Page 456.

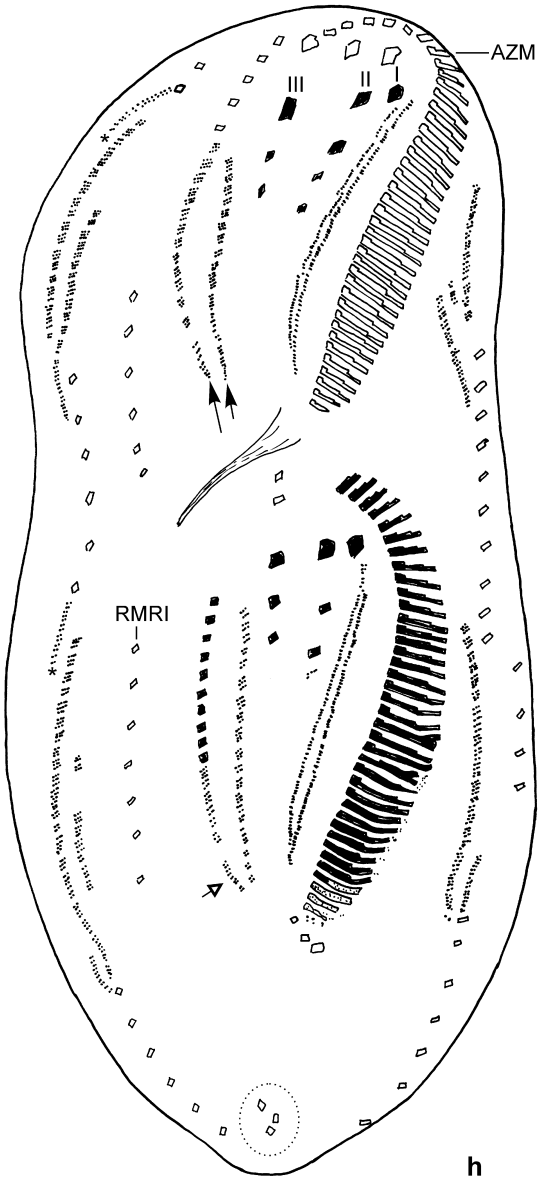

Fig. 80h *Fragmocirrus espeletiae* (after Foissner 2000. Protargol impregnation). Infraciliature of ventral side of middle divider, 196 µm. Short arrow marks new left, long arrow marks new right frontoventral row of proter. Asterisks mark rear end of new dorsomarginal kineties (= new dorsal kineties 4). Parental pretransverse ventral and transverse cirri circled. According to the original description only the rear portion of the right frontoventral row (open arrow) forms transverse cirri; however, the arrangement and the fine structure (Fig. 80f3) strongly indicates that one transverse cirrus is formed from the left frontoventral row anlage and each one pretransverse ventral and transverse cirrus by the right frontoventral row anlage. AZM = parental adoral zone of membranelles, RMRI = rear portion of parental inner right marginal row, I–III = frontal-ventral cirri anlagen I–III. Page 456.

407, 422) and the oxytrichids *Paraurostyla weissei* (for review, see Berger 1999, p. 844) and *Parentocirrus hortualis* (for review, see Berger 1999, p. 879; Blatterer & Foissner 2003). However, as discussed in the remarks, only *Parakahliella* is closely related to *Fragmocirrus*, that is, the similarity with *Paraurostyla* and *Parentocirrus*

is very likely based on plesiomorphies or convergencies. For a detailed documentation of the ontogenesis, see Fig. 54–83 in Foissner (2000).[1]

The oral primordium originates left of the posterior two thirds of the left frontoventral row. The cirri are, however, not involved in the oral primordium formation. Somewhat later these cirri are the basis for the formation of the anlagen for the left and right frontoventral row of the opisthe. The formation of the new adoral zone and undulating membranes proceeds as in *Parakahliella*. The unaltered parental adoral zone is taken over by the proter, while the parental undulating membranes and pharyngeal fibres are reorganised (Fig. 80h).

Usually, *Fragmocirrus espeletiae* produces each five frontal-ventral-transverse cirri anlagen in both filial products. Sometimes one or two extra primordia of varying length appear between the anlagen III and that for the right frontoventral row. The number of cirri formed in the anlagen for the left and right frontoventral row is highly variable. These irregularities are partly responsible for the considerable total variability of the cirral pattern of *F. espeletiae*. Very likely, no or only few parental cirri are preserved in the following generation. The cirral anlagen for the proter originate as follows (produced part of ciliature in brackets): anlage I – primordium for undulating membranes (left frontal cirrus); anlage II – buccal cirri (middle frontal cirrus and buccal cirri); anlage III – parabuccal cirri, rearmost cirrus likely not involved in anlagen formation (right frontal cirrus and parabuccal cirri). The anlagen for the left and right frontoventral row are formed as follows: (i) A single streak originates within the right frontoventral row. Subsequently, the posterior third of this streak moves rightwards and produces basal bodies eventually forming a second streak. These two anlagen form roughly a V-shaped pattern, the left one becomes the left frontoventral row, the right one the right frontoventral row (Fig. 80h). The foremost four (range 3–6) and hindmost one (range 1–4) cirrus of the right frontoventral row do not contribute to primordia formation and are resorbed during cell division (Fig. 80h). According to the original description, the posterior portion of the anlage for the right frontoventral row separates and migrates posteriorly to form the inconspicuous transverse cirri (Fig. 80h, open arrow). I suppose that this anlage produces a transverse cirrus and a pretransverse ventral cirrus; the left transverse cirrus is likely formed by the anlage for the left frontoventral row. This assumption is based on the arrangement and fine structure of the cirri (Fig. 80f3). Unfortunately, the stage showing this part of the division cycle is not available.

The anlagen I–III of the opisthe are formed, as is usual, by the oral primordium. The anlagen for the left and right frontoventral row originate from the middle portion of the parental left frontoventral row. As in the proter, the primordia for the left and right frontoventral row form a V-shaped pattern. Later, the anlage for the left row migrates posteriorly to form the final pattern. The anteriormost and posteriormost 2–5 cirri of the parental row are not involved in anlagen formation (Fig. 80h).

[1] It would have been very expensive to get the permissions to reproduce the illustrations. Thus, I made redrawings of the interphasic illustrations and a late divider.

Table 24 Morphometric data on *Fragmocirrus espeletiae* (from Foissner 2000)

Characteristics [a]	mean	M	SD	SE	CV	Min	Max	n
Body, length	155.9	150.0	31.5	6.9	20.2	122.0	264.0	21
Body, width	64.5	59	18.0	3.9	27.9	38.0	105.0	21
Adoral zone of membranelles, length	53.9	50.0	13.4	2.9	24.9	40.0	100.0	21
Macronuclear nodule, length [b]	17.4	18.0	3.3	0.7	19.2	12.0	23.0	21
Macronuclear nodule, width [b]	11.1	11.0	3.5	0.8	31.4	6.0	20.0	21
Macronuclear nodules, number	4.2	4.0	0.5	0.1	12.7	4.0	6.0	21
Micronuclei, length	3.9	4.0	0.8	0.2	20.7	3.0	6.0	21
Micronuclei, width	3.2	3.0	–	–	–	3.0	4.0	21
Micronuclei, number	2.5	2.0	1.0	0.2	39.6	1.0	6.0	21
Adoral membranelles, number	37.5	36.0	5.3	1.2	14.0	30.0	50.0	21
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	0.3.0	3.0	21
Buccal cirri, number	3.1	3.0	0.6	0.1	20.4	2.0	5.0	26
Ventral cirral rows, number [c]	5.0	5.0	0.0	0.0	0.0	5.0	5.0	21
Left frontal cirrus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Middle frontal cirrus plus buccal cirri, number	3.9	4.0	0.6	0.1	14.8	3.0	5.0	30
Right frontal cirrus plus parabuccal cirri, number	3.7	4.0	–	–	–	3.0	4.0	30
Left frontoventral row, number of cirri	17.8	18.0	2.7	0.6	15.0	13.0	25.0	21
Right frontoventral row, number of cirri	14.4	14.0	2.3	0.5	15.8	11.0	20.0	21
Transverse cirri, number [d]	3.0	3.0	–	–	–	3.0	4.0	25
Left marginal rows, number	1.5	2.0	–	–	–	1.0	2.0	30
Inner left marginal row, number of cirri	30.1	30.0	3.1	0.7	10.2	25.0	37.0	21
Outer left marginal row, number of cirri	6.6	5.0	5.0	0.9	75.1	1.0	25.0	30
Right marginal rows, number	1.9	2.0	–	–	–	1.0	2.0	30
Outer right marginal row, number of cirri	31.8	31.0	3.1	0.7	9.7	27.0	39.0	21
Inner right marginal row, number of cirri	12.3	12.0	9.1	2.0	74.3	1.0	34.0	21
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Caudal cirri, number	3.2	3.0	0.6	0.1	18.4	2.0	5.0	25

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] Nodule measured (anteriormost, posteriormost, ...) not indicated.

[c] Including (i) left frontal cirrus, (ii) middle frontal cirrus and buccal cirri, and (iii) right frontal cirrus and parabuccal cirri.

[d] I suppose that one pretransverse ventral cirrus and two transverse cirri are present (Fig. 80f3).

In the outer right and the (inner) left marginal row each two anlagen – the anterior for the proter, the posterior for the opisthe – are formed. In middle dividers, one or more short primordia develop near the rear end of each; further, at the anterior end of the right anlage basal body pairs are produced to form the dorsomarginal kinety (Fig. 80h). The short, rear primordia became the inner right and the outer left marginal rows. Foissner (2000) could not clarify whether the anlagen split off from the regular (outer right and inner left) marginal primordia or emerge directly from parental marginal cirri. The interphasic variability of the cirral pattern is rather high because the outer left marginal cirri anlagen are often lacking and the inner right mar-

ginal anlagen/rows are of rather different length (Table 24). The primordia at the anterior end of the right marginal row anlagen become the dorsomarginal kineties, that is, the new kinety 4 of each filial product.

The dorsal ciliature is formed in the *Urosomoida* pattern (Berger 1999, p. 73; = type 2 pattern of Foissner & Adam 1983), which is also present in *Afrokahliella*. Briefly, within parental kineties 1–3 each one anlage originates for the proter and the opisthe, and from/near the anterior end of the new right marginal row one dorsomarginal kinety (= kinety 4) is formed (Foissner 2000). By contrast, in *Parakahliella* a parental kinety is retained in each divider so that these species have in total five dorsal kineties. As is usual in *Parakahliella*-like taxa, caudal cirri originate at the end of dorsal kineties 1 (usually two cirri) and 2 (usually one) so that in total three caudal cirri are present on average in *Fragmocirrus*.

The nuclear apparatus divides alike as in most other hypotrichs, that is, the nodules fuse to a globular mass, which later divides three, rarely four times to form the characteristic nuclear pattern. The micronuclei divide mitotically without fusion.

Occurrence and ecology: *Fragmocirrus espeletiae* is perhaps confined to terrestrial habitats in America. The type locality is about 2 km east of the Pico del Aquila (08°52'N 70°48'W), Páramo de Piedras Blancas, Cordillera de Mérida in Venezuela, where Foissner (2000) discovered it on decaying leaves from dead, rotting *Espeletia* trunks. The material (pH 6.0) was very likely 100–150 years old and the leaves, respectively, the trunk were partially covered with a greenish layer of algae and some small mosses; soil particles and excrement of microarthropods had accumulated between the leaves (Foissner 2000, p. 54).

Fragmocirrus espeletiae feeds on heterotrophic flagellates and small (*Colpoda steinii*) and middle-sized ciliates such as *Colpoda lucida* and *Gonostomum affine* (Foissner 2000).

Perisincirra Jankowski, 1978

1978 ***Perisincirra* gen. n.** – Jankowski, Tezisy Dokl. zool. Inst. Akad. Nauk SSSR, year 1978: 40 (original description): Type (by original designation): *Uroleptus kahli* Grolière, 1975.

1979 ***Perisincirra* Jk., 1978** – Jankowski, Trudy zool. Inst., 86: 61 (generic catalogue of hypotrichs).

1985 ***Perisincirra***[1] – Small & Lynn, Phylum Ciliophora, p. 457 (guide to ciliate genera).

1987 ***Perisincirra* Jankowski, 1979** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (classification of hypotrichs; incorrect year).

1994 ***Perisincirra* Hemberger, 1985** – Tuffrau & Fleury, Traite de Zoologie, 2: 143 (classification of hypotrichs; incorrect author and year).

2001 ***Perisincirra* Jankowski 1978** – Aescht, Denisia, 1: 124 (catalogue of generic names of ciliates).

2001 ***Perisincirra* Jankowski, 1978** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 71 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2007 ***Perisincirra* Jankowski, 1979** – Jankowski, Phylum Ciliophora, p. 461 (generic revision of ciliates; see nomenclature).

[1] Small & Lynn (1985) provided the following characterisation: 0–1 other frontal cirri neither in transverse cirral row, nor in longitudinal file.

2008 ***Perisincirra* Jankowski, 1978** – Lynn, Ciliated protozoa, p. 362 (familial revision of ciliates).

Nomenclature: No derivation of the genus-group name is given in the original description or a later paper. Unfortunately, I cannot provide a meaningful explanation because I do not understand the meaning of the middle part *sin-* in the present context; according to Werner (1972, p. 376), the stem *sin-* means damage or to damage, which makes no sense; perhaps a deviating spelling of the Greek *syn-* (together with); needs further analysis. Feminine gender (Aescht 2001, p. 294). According to Aescht (2001), the type fixation is by monotypy because only one species was originally included. I suppose that it is by original designation because Jankowski (1978) wrote "*Perisincirra* gen. n. for *Uroleptus kahli* Grolière". Jankowski (2007), the author of the genus, used 1979 and not 1978 as date, perhaps because the "diagnosis"[1] in Jankowski (1978) is rather meagre. Incorrect subsequent spelling: *Perisincira* (Tirjaková 1988, p. 500; Szabó 1999, p. 249; 2000a, p. 8).

Characterisation (A = supposed apomorphy): Kahliellidae(?). Adoral zone of membranelles and even undulating membranes roughly in *Gonostomum*-pattern. Each two or more cirral rows right and left of midline, cirri within all rows very widely spaced (A). Three frontal cirri, buccal and parabuccal cirrus/cirri present. Frontoterminal, postoral ventral, pretransverse ventral, and transverse cirri lacking (A?). Three (*P. kahli*, *P. paucicirrata*?) or four (*P. longicirrata*, including one dorsomarginal[?] kinety) dorsal kineties; caudal cirri likely present.[2] Limnetic and terrestrial.

Additional characters: For the type species life data are more or less lacking. Thus, the present chapter is rather short. Body very flexible, acontractile. Two macronuclear nodules. Cortical granules likely lacking. Undulating membranes more or less straight and relatively short. Most cirri rather fine and long (*P. paucicirrata*, *P. longicirrata*). Dorsal bristles short (about 3–5 µm).

Remarks: The species now assigned to this genus are not common and therefore little known. Grolière (1975, p. 497) classified the type species of *Perisincirra* (*U. kahli* Grolière, 1975) in *Uroleptus*, a genus assigned to the Holostichidae by Borror (1972), the main revision to which Grolière referred.[3] Jankowski (1978) recognised the incorrect generic placement of this species and therefore established the monotypic genus *Perisincirra*. Jankowski (1979, p. 78) assigned it to the Psammomitrinae Jankowski, 1979, a synonym (or monotypical subgroup?) of the Holostichidae according to Berger (2006a, p. 85, 227), a valid taxon according to Yi et al. (2009).

Hemberger (1982, p. 134, 206) reviewed *Perisincirra* Jankowski and assigned it to the oxytrichids. Unfortunately, he incorrectly assumed that *Uroleptus kahli* Buitkamp, 1977, the junior homonym of *U. kahli* Grolière, 1975 is the type species. Via

[1] The diagnosis is in Russian. I suppose that Jankowski (1978) removed *U. kahli* Grolière from *Uroleptus* because of the lacking midventral complex.

[2] The dorsal infraciliature of the two slender species (*P. kahli* and *P. paucicirrata*) is not known in detail. Thus, this feature needs revaluation when further data are available.

[3] Since several years it is known that *Uroleptus* is a non-oxytrichid dorsomarginalian species, while the holostichids branch off at the base of the Hypotricha tree (Foissner et al. 2004, Berger 2008).

a personal communication from Jankowski to Buitkamp (a colleague of Hemberger at the Bonn University), Hemberger knew that Jankowski has proposed a replacement name (*Perisincirra buitkampi*) for *U. kahli* Buitkamp, 1977 (Hemberger 1982, p. 134). He discussed that the replacement name is not justified because this would presuppose an older *P. kahli*.[1] Simultaneously, Hemberger (1982, p. 278) listed the senior homonym *U. kahli* Grolière, 1975 – the true type species of *Perisincirra* – as species which cannot be assigned to a certain higher taxon. Since *Perisincirra* in Hemberger (1982) does not include the type species, Hemberger's thesis is not mentioned in the list of synonyms. Somewhat later, Hemberger (1985, p. 408) recognised the mistake and validly published the "*Perisincirra*" species described in his dissertation in the genus *Hemisincirra* Hemberger, 1985 (for review, see Berger 2008, p. 387).

Foissner (1982, p. 66) established the genus *Engelmanniella* with *Uroleptus mobilis* Engelmann, 1862 as type species (p. 502). In addition, he transferred *U. kahli* Grolière, 1975 – the type species of *Perisincirra* Jankowski, 1978 – to *Engelmanniella*, which he classified in the Oxytrichidae, however, with doubt. Thus, he put (probably unknowingly) *Perisincirra* Jankowski, 1978 into the synonymy of his new genus producing a very tricky nomenclatural situation, all the more, considering that he also accepted *Perisincirra* (Foissner 1982, p. 87). Very likely, this mistake was due to the fact that Foissner (1982) took over the diagnosis and type species of *Perisincirra* Jankowski, 1978 from Hemberger (1982, p. 206), who incorrectly assumed that *Uroleptus kahli* Buitkamp, 1977 is the type (see above). Somewhat later, Foissner (1984, p. 119) recognised the inconsistency and listed the correct type species of *Perisincirra* (type *U. kahli* Grolière, 1975), *Engelmanniella* (*U. mobilis* Engelmann, 1862), and *Hemisincirra* (*U. kahli* Buitkamp, 1977), that is, he removed *U. kahli* Grolière from *Engelmanniella*.

Curds et al. (1983, p. 420) discussed under the heading of *Uroleptus* Ehrenberg, 1831 that Jankowski (1978) has created *Perisincirra* for *Uroleptus kahli* Grolière, 1975. Since they provided Fig. 81a (*U. kahli* Grolière) with the legend *Uroleptus*, one has to conclude that they put *Perisincirra* – together with *Platytrichotus* Stokes, 1886 – into the synonymy of *Uroleptus*, a proposal which is certainly incorrect because *Uroleptus* has a very pronounced midventral pattern (see below).

Small & Lynn (1985) classified *Perisincirra* in the Cladotrichidae, a group later submerged in the Kahliellidae by Lynn (2008, p. 357). Unfortunately, they adduced as instances *Perisincirra similis* Foissner, 1982 (now *Hemiurosoma similis*; for review, see Berger 2008, p. 633) and *Perisincirra gracilis* Foissner, 1982 (now *Caudiholosticha gracilis*; for review, see Berger 2006a, p. 266), and not the type species *P. kahli*.

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[1] The statement of Hemberger (1982) is basically correct because the primary homonymy does not exist in *Perisincirra*, but in *Uroleptus*. Thus, Jankowski (1979) should have introduced the replacement name in *Uroleptus*, and not in *Perisincirra*. However, Jankowski (1979) is also right in that a junior primary homonym is permanently invalid and has to be replaced (ICZN 1999, Article 57.2; Article 23.9.5 obviously refers to pre-1900 homonyms).

Table 25 Morphometric data on *Perisincirra kahli* (kah, from Grolière 1975), *Perisincirra longicirrata* (lon, type population from Foissner et al. 2002a), and *Perisincirra paucicirrata* (pau, type population from Foissner et al. 2002a)

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Body, length	kah	115.0	–	–	–	–	85.0	160.0	?
	lon	71.2	70.0	9.1	2.3	12.8	53.0	92.0	16
	pau	84.8	87.0	13.3	3.0	15.7	64.0	121.0	20
Body, width	kah	–	–	–	–	–	7.0	12.0	?
	lon	33.0	32.0	5.8	1.4	17.5	24.0	50.0	16
	pau	21.9	22.0	3.9	0.9	17.7	14.0	32.0	19
Body length:width, ratio	kah	–	–	–	–	–	10.0	15.0	?
	lon	2.2	2.2	0.3	0.1	11.5	1.8	2.6	16
	pau	4.1	3.9	1.3	0.3	32.6	2.2	8.6	19
Adoral zone of membranelles, length	kah	18.5	–	–	–	–	16.0	20.0	?
	lon	25.9	25.5	3.3	0.8	12.8	22.0	32.0	16
	pau	14.8	15.0	1.0	0.2	7.0	13.0	16.0	19
Body length:length of adoral zone, ratio	lon	2.8	2.7	0.4	0.1	13.2	2.3	3.5	16
	pau	5.8	5.8	1.3	0.3	21.9	4.0	9.3	19
Anterior body end to buccal cirrus, distance	lon	13.2	14.0	2.2	0.6	16.7	10.0	18.0	15
	pau	5.8	6.0	0.7	0.2	12.5	5.0	7.0	17
Anterior body end to first macronuclear nodule, distance	lon	18.3	18.0	3.1	0.8	17.1	14.0	24.0	16
	pau	23.1	24.0	4.1	0.9	17.8	16.0	31.0	19
Macronuclear nodules, distance in between	lon	7.2	8.0	3.4	0.9	47.4	1.0	12.0	16
	pau	6.2	6.0	3.1	0.7	50.5	2.0	14.0	19
Anterior macronuclear nodule, length	kah [b]	29.0	–	–	–	–	–	–	?
	lon	15.4	14.0	2.5	0.6	16.3	12.0	21.0	16
	pau	12.8	12.0	2.6	0.6	20.1	10.0	19.0	19
Anterior macronuclear nodule, width	kah [b]	2.0	–	–	–	–	–	–	?
	lon	6.6	6.5	1.1	0.3	16.4	5.0	9.0	16
	pau	4.1	4.0	1.0	0.2	25.3	2.5	6.0	19
Posterior macronuclear nodule, width	lon	14.5	14.5	1.9	0.5	13.3	11.0	17.0	16
	pau	12.3	12.0	2.0	0.5	16.0	9.0	17.0	19
Posterior macronuclear nodule, width	lon	6.4	6.0	1.2	0.3	18.9	5.0	10.0	16
	pau	3.4	3.0	0.8	0.2	23.1	2.5	6.0	19
Anterior body end to paroral, distance	lon	11.4	10.5	2.4	0.7	21.4	8.0	16.0	14
	pau	5.1	5.0	0.8	0.2	15.8	4.0	6.0	15
Anterior body end to endoral, distance	lon	15.2	14.0	2.6	0.7	17.1	12.0	20.0	15
	pau	6.5	6.0	0.7	0.2	10.2	6.0	8.0	13
Paroral, length	lon	8.3	8.0	1.5	0.4	18.7	5.0	11.0	12
	pau	5.5	5.0	–	–	–	5.0	6.0	11
Endoral, length	lon	9.8	10.0	1.5	0.4	15.2	7.0	12.0	13
	pau	6.8	7.0	–	–	–	6.0	8.0	12
Macronuclear nodules, number	kah	2.0	–	–	–	–	–	–	?
	lon	2.0	2.0	0.0	0.0	0.0	2.0	2.0	16
	pau	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Anterior micronucleus, length	kah	4.0	–	–	–	–	–	–	?
	lon	3.0	3.0	–	–	–	2.5	4.0	15
Anterior micronucleus, width	kah	4.0	–	–	–	–	–	–	?
	lon	2.7	2.5	–	–	–	2.0	4.0	15
Micronuclei, number	kah	2.0	–	–	–	–	–	–	?
	lon	1.9	2.0	–	–	–	1.0	2.0	16
	pau	1.0	1.0	0.0	0.0	0.0	1.0	1.0	5

Table 25 Continued

Characteristics [a]	Species	mean	M	SD	SE	CV	Min	Max	n
Adoral membranelles, number	lon	21.0	21.0	1.0	0.3	4.9	18.0	22.0	16
	pau	15.2	15.0	1.0	0.2	6.8	13.0	17.0	19
Frontal cirri, number	kah	3.0	–	–	–	–	–	–	?
	lon	3.0	3.0	0.0	0.0	0.0	3.0	3.0	16
	pau	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
Buccal cirri, number	kah	1.0	–	–	–	–	–	–	?
	lon	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	pau	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Parabuccal cirri, number	lon	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	pau	2.0	2.0	–	–	–	1.0	3.0	18
Cirral rows right of midline, number	kah	2.0	–	–	–	–	–	–	?
	lon	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
	pau	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Cirral rows left of midline, number	lon	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
	pau	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Right cirral row 1, number of cirri [b]	lon	10.5	11.0	1.5	0.4	14.4	7.0	12.0	13
	pau	8.9	9.0	1.8	0.4	19.7	5.0	12.0	18
Right cirral row 2, number of cirri [b]	kah	–	–	–	–	–	18.0	20.0	?
	lon	11.9	12.0	1.3	0.4	11.1	9.0	14.0	13
	pau	6.3	7.0	1.2	0.3	19.5	4.0	8.0	18
Right cirral row 3, number of cirri [b]	lon	11.6	12.0	2.3	0.6	20.0	7.0	16.0	13
Left cirral row 1, number of cirri [b]	lon	7.7	7.0	2.5	0.8	33.3	5.0	14.0	9
	pau	5.7	6.0	1.5	0.4	26.7	3.0	9.0	18
Left cirral row 2, number of cirri [b]	kah	–	–	–	–	–	16.0	20.0	?
	lon	8.1	8.0	1.7	0.5	21.0	4.0	10.0	11
	pau	6.5	7.0	1.0	0.2	15.4	5.0	8.0	17
Left cirral row 3, number of cirri [b]	lon	7.2	7.0	2.0	0.6	28.4	3.0	10.0	13
Dorsal kineties, number	kah	3.0	–	–	–	–	–	–	?
	lon	4.0	4.0	0.0	0.0	0.0	4.0	4.0	10
	pau	3.0			(see text)				
Caudal cirri, number	lon	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known: when two values are known, they are listed as Min and Max; when only one value is given, it is listed as mean), SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] Macronuclear nodule (anterior/posterior) not specified.

[c] Cirral rows are numbered from inside to outside.

Tuffrau (1987) was the first who assigned *Perisincirra* to the Kahliellidae, a classification taken over by Jankowski (2007). Interestingly, Tuffrau & Fleury (1994) removed it from the kahliellids and put it into the Oxytrichidae, which is, however, not justified at the present state of knowledge because a dorsal kinety fragmentation, the main feature of this group, is very likely lacking.

Shi et al. (1999, p. 124) and Shi (2000, p. 12) classified *Perisincirra* Jankowski, 1978 as synonym of *Hemisincirra* Hemberger, 1985, an act which is both nomenclaturally (disregard of the principle of priority) as well as taxonomically incorrect (see below).

Lynn (2008) classified *Perisincirra* in the Urostylidae, perhaps because the type species (*Uroleptus kahli* Grolière, 1975) has been originally described in *Uroleptus*, a genus previously always assigned to the urostyloids. However, now we know that *Uroleptus* is not closely related to the urostyloids because of morphological and molecular differences (Foissner et al. 2004, Berger 2006a, p. 37).

Some papers dealing with *Perisincirra* are not included in the list of synonyms because none of the species described therein belongs to *Perisincirra* (e.g., Foissner 1982, Dragesco & Dragesco-Kernéis 1986).

As mentioned above, *Perisincirra* was assigned to five different higher taxa so far, namely the Oxytrichidae, the Psammomitrinae, the Cladotrichidae, the Kahliellidae, and the Urostylidae. This high "diversity" clearly shows the uncertainty as concerns the phylogenetic position of this genus. Unfortunately, I am also uncertain about the taxonomic placement, especially because we lack some important morphological/morphogenetic data and molecular analyses of the type species. A position in the Oxytrichidae is unlikely because *P. kahli* has three dorsal kineties, indicating that the ordinary bipolar rows of the ground pattern are present, that is, a dorsal kinety fragmentation – which is so characteristic for the oxytrichids – is (very likely) lacking (Berger 1999, 2006a, 2008).

Psammomitra, the name-bearing type of the Psammomitrinae, is a urostyloid, a large group of hypotrichs branching off rather basally, and morphologically characterised by an urostyloid midventral pattern and the plesiomorphic dorsal kinety pattern (for review, see Berger 2006a). Since a zigzagging midventral pattern is lacking in *P. kahli* and the other two species assigned to *Perisincirra*, a classification in the urostyloids is out of the question.

Cladotricha, the name-bearing type of the Cladotrichidae, is preliminary classified in the Gonostomatidae because of similarities in the oral apparatus (p. 235). Admittedly, the oral apparatus of the three *Perisincirra* species is also somewhat reminiscent of that of *Gonostomum* (see descriptions). In addition, *P. kahli* (and likely *P. paucicirrata* too) probably has the same plesiomorphic dorsal infraciliature (three bipolar kineties) so that a classification of the present genus in the Gonostomatidae would be an alternative. However, none of the taxa included in the gonostomatids has the widely spaced cirri of *Perisincirra*. Thus, I preliminary follow Tuffrau (1987) and classify *Perisincirra* in the Kahliellidae, mainly for practical reasons because the wide distance between the cirri in *Kahliella* and *Perisincirra* is not a homology. In *Kahliella* the rows with widely spaced cirri are remnants from the parental generations whereas in *Perisincirra* the cirri are primarily widely spaced.

In the original description of *P. paucicirrata* we argued that *Perisincirra* belongs to the Kahliellidae because of the four cirral rows and the lack of transverse and midventral cirri (Foissner et al. 2002a). However, we overlooked that *Kahliella sim-*

plex, a species perhaps synonymous with the type of *Kahliella*, has a dorsomarginal row which is lacking in *P. kahli* (type of *Perisincirra*) and *P. paucicirrata* (has to be confirmed), but very likely also present in *P. longicirrata* (Fig. 83e). This inhomogeneity shows that the classification of *Perisincirra* in the Kahliellidae is very uncertain and that *P. longicirrata* is possibly not congeneric with *P. kahli* and *P. paucicirrata* (see below).

In the 1980s, *Perisincirra* was a melting pot mainly containing slender, terrestrial hypotrichs with a short to moderately long, continuous or slightly irregular frontoventral row (Hemberger 1982, Foissner 1982). Foissner (1984) and Hemberger (1985) recognised that they have oriented on the incorrect type species (*U. kahli* Buitkamp, 1977). Therefore, Hemberger (1985) introduced the genus *Hemisincirra* with *U. kahli* Buitkamp as type species (see above and review by Berger 2008, p. 387), and Foissner (1984) and Hemberger (1985) removed all species, except for *P. kahli* (Grolière, 1975), from *Perisincirra*. Since then, *Perisincirra* was a little known, monotypic genus and just Foissner et al. (2002a) basically could confirm this genus in that they found two new species, namely *P. paucicirrata* and *P. longicirrata*. The type species of *Hemisincirra* (*H. buitkampi*) and *Perisincirra* (*P. kahli*) are little known making the morphological characterisation and the estimation of the phylogenetic positions of these two genera rather difficult. *Hemisincirra* is preliminary classified in the Amphisiellidae (details see Berger 2008, p. 387). It differs from *Perisincirra* mainly in the number of cirral rows (two long rows[1] vs. four or six rows) and the transverse cirri (present [difficult to recognise] vs. absent). Buitkamp (1977) described the lack of caudal cirri for *H. buitkampi*, whereas Grolière (1975) made no comment about this part of the dorsal infraciliature. However, *Perisincirra paucicirrata*, which is very similar to *P. kahli*, very likely (Fig. 82d, f), and *P. longicirrata* (classification in *Perisincirra* not certain) certainly has caudal cirri (Fig. 83e). Thus, a synonymy of *Hemisincirra* and *Perisincirra* can almost be excluded. For separation of *Perisincirra* from *Engelmanniella*, see *P. kahli*. *Neogeneia* (p. 481) and *Deviata* (p. 555) species have a higher number of cirral rows and more tightly spaced cirri in at least some of the rows (Foissner et al. 2002a).

The three species now included in *Perisincirra* basically agree in the ventral cirral pattern, especially in the widely spaced cirri within the individual rows. However, *Perisincirra longicirrata* differs from the other two species by several features (body shape, number of cirral rows, size and shape of oral apparatus), including the dorsal kinety pattern (dorsomarginal row very likely present vs. very likely absent). Thus, the inclusion of *P. longicirrata* in the present genus is uncertain. The dorsal kinety pattern of all *Perisincirra* species has to be studied in detail (including morphogenesis to know whether or not kinety 4 of *P. longicirrata* is indeed a dorsomarginal kinety), and the gene sequences have to be analysed to get a better insight into the phylogenetic relationships of these species. I suspect that *P. longicirrata* is misclassified in the present genus, but do not establish a new genus because some data are lacking.

[1] In few *Hemisincirra* species one moderately long (less then 50% of body length) frontoventral row is present (Berger 2008, p. 387).

Perisincirra species invariably have four (type and *P. paucicirrata*) or six (*P. longicirrata*) cirral rows with widely spaced cirri. Since the wide distance between the individual cirri is equal in all rows we have to assume that this is a specific feature of *Perisincirra*, and not due to the preservation of parental cirri in the next generation, as, for example, in *Kahliella* or *Engelmanniella*. The rows on the left side are certainly marginal rows. Whether the inner (type and *P. paucicirrata*) or inner one or two (*P. longicirrata*) right rows are also marginal rows or (a) frontoventral row(s) is not known. When the rows are indeed marginals, then *Perisincirra* would have only three frontoventral anlagen, certainly an apomorphy. However, ontogenetic data are needed for a final (or at least more proper) decision. Heretofore, the neutral formulation right and left cirral rows is used; numbering is from inside to outside (e.g., Fig. 82c).

Species included in *Perisincirra* (alphabetically arranged basionyms are given): (1) *Perisincirra paucicirrata* Foissner, Agatha & Berger, 2002a; (2) *Perisincirra longicirrata* Foissner, Agatha & Berger, 2002a; (3) *Uroleptus kahli* Grolière, 1975 (type species).

Species misplaced in *Perisincirra*: The following species – largely originally classified in *Perisincirra* – are now assigned to other genera, mainly to *Hemisincirra* Hemberger, 1985. If you do not find a certain name in the list below, see the index.

Perisincirra buitkampi Jankowski, 1979. Remarks: Now *Hemisincirra buitkampi* (Jankowski, 1979) Berger, 2008 (for review, see Berger 2008, p. 393; type of *Hemisincirra*).

Perisincirra filiformis Foissner, 1982. Remarks: Now *Circinella filiformis* (Foissner, 1982) Foissner, 1994a (p. 333).

Perisincirra gellerti Foissner, 1982. Remarks: Now *Hemisincirra gellerti* (Foissner, 1982) Foissner in Berger, 2001 (for review, see Berger 2008, p. 424).

Perisincirra gracilis Foissner, 1982. Remarks: Now *Caudiholosticha gracilis* (Foissner, 1982) Berger, 2006a (for review, see Berger 2006a, p. 266).

Perisincirra heterocirrata Hemberger, 1982. Remarks: This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3). Now *Anteholosticha heterocirrata* (Hemberger, 1985) Berger, 2008 (for review, see Berger 2008, p. 640).

Perisincirra inquieta Hemberger, 1982. Remarks: This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3). Now *Hemisincirra inquieta* Hemberger, 1985 (for review, see Berger 2008, p. 403).

Perisincirra interrupta Foissner, 1982. Remarks: Now *Hemisincirra interrupta* (Foissner, 1982) Foissner in Berger 2001 (for review, see Berger 2008, p. 432).

Perisincirra kahli (Buitkamp, 1977) Hemberger, 1982. Remarks: This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3). Now *Hemisincirra buitkampi* (Jankowski, 1979) Berger, 2008 (for review, see Berger 2008, p. 393; type of *Hemisincirra*).

Perisincirra octonucleata Hemberger, 1982. Remarks: This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3). Now *Hemisincirra octonucleata* Hemberger, 1985 (for review, see Berger 2008, p. 421).

Perisincirra pori Wilbert & Kahan, 1986. Remarks: Now *Lamtostylides pori* (Wilbert & Kahan, 1986) Berger, 2008 (for review, see Berger 2008, p. 344).

Perisincirra quadrinucleata Hemberger, 1982. Remarks: This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3). Now *Hemisincirra quadrinucleata* Hemberger, 1985 (for review, see Berger 2008, p. 419).

Perisincirra similis Foissner, 1982. Remarks: Now *Hemiurosoma similis* (Foissner, 1982) Foissner, Agatha & Berger, 2002a (for review, see Berger 2008, p. 633).

Perisincirra vermicularis Hemberger, 1982. Remarks: This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3). Now *Hemisincirra vermicularis* Hemberger, 1985 (for review, see Berger 2008, p. 435).

Perisincirra viridis Foissner, 1982. Remarks: Now *Terricirra viridis* (Foissner, 1982) Berger & Foissner, 1989a (for review, see Berger 2008, p. 450).

Key to *Perisincirra* species

If you cannot identify your specimen/population with the key below, see also keys to *Engelmanniella* (p. 498) or *Hemisincirra* (Berger 2008, p. 392).

1 Body very slender (length:width ratio about 10–15:1; Fig. 81a). . . . . *Perisincirra kahli* (p. 471)

\- Body not very slender (Fig. 82a, 83a). **2**

2 Body length:width ratio about 5:1; each two cirral rows right and left of midline; single micronucleus in between macronuclear nodules; cirri about 15 µm long (Fig. 82a–f). . . . . *Perisincirra paucicirrata* (p. 474)

\- Body length:width ratio about 3:1; each three cirral rows right and left of midline; nuclear apparatus not as above (each macronuclear nodule with a micronucleus); cirri about 20–30 µm long (Fig. 83a–e). . . . . *Perisincirra longicirrata* (p. 477)

Perisincirra kahli (Grolière, 1975) Jankowski, 1978
(Fig. 81a, Table 25)

1975 ***Uroleptus khali* n. sp.** – Grolière, Protistologica, 11: 482, Fig. 2, 10 (Fig. 81a; original description; site where type material deposited not mentioned, perhaps in Station Biologique de Besse-en-Chandesse, France, where Grolière worked; incorrect original spelling, see nomenclature).

1978 ***Uroleptus kahli* Grolière** – Tezisy Dokl. zool. Inst.Akad. Nauk SSSR, 1978: 40 (fixation as type species of *Perisincirra*; see nomenclature).

1982 ***Engelmanniella kahli* (Grolière, 1975) nov. comb.** – Foissner, Arch. Protistenk., 126: 66 (comparison with *Engelmanniella mobilis* and combination with *Engelmanniella* Foissner, 1982).

1983 ***Uroleptus kahli* Grolière, 1975** – Curds, Gates & Roberts, British and other freshwater ciliated protozoa, p. 420, Fig. 249A (redrawing[?] of Fig. 81a; guide to freshwater genera).

2001 ***Perisincirra kahli* (Grolière, 1975) Jankowski, 1978** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 98 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: Grolière (1975) provided, obviously par lapsus, two different original spellings, namely, *Uroleptus khali* in the heading (p. 482) and the text (p. 483), and *Uroleptus kahli* in the abstract (p. 481), the legends (p. 483, 489), and the discussion (p. 497). Although he did not provide an etymology it is evident that he dedicated this species to Alfred Kahl, the great German ciliatologist, that is, *Uroleptus kahli* is the correct original spelling, which was also used by Jankowski (1978, 1979). For homonymy with *U. kahli* Buitkamp, 1977, see Berger (2008, p. 394).

Jankowski (1978) fixed *U. kahli* Grolière as type species of *Perisincirra*, but did not formally transfer it to the new genus. However, due to the type fixation he is automatically the combining author, as indicated in the heading.

Jankowski (1979, p. 61) mentions "*Uroleptopsis kahli*, ibidem"[1] under the heading *Perisincirra*, meaning that Grolière (1975) has used this combination. Previously, I could not explain this combination and thought that Jankowski (1979) has made it (Berger 2001, p. 98; 2006a, p. 986). Now I suppose that "*Uroleptosis kahli*" in Grolière (1975, p. 497; incorrect subsequent spelling of *Uroleptopsis*!) is only a misspelling of "*Uroleptopsis* Kahl" because in this sentence he compared *Uroleptus kahli* with *Uroleptopsis* Kahl, 1932, a pseudokeronopsid urostyloid without transverse cirri (Berger 2004; 2006a, p. 980). A species "*Uroleptopsis kahli*" was never described.

Remarks: Grolière (1975) classified this species in *Uroleptus*, likely because of the slender body and the ventral rows. Unfortunately, some important data (e.g., presence/absence of cortical granules, exact dorsal infraciliature) are not described preventing a serious characterisation of the genus *Perisincirra* (see above). Foissner (1982) was sure that it belongs to *Engelmanniella* because of similarities in the cirral pattern with the type species *E. mobilis* (see genus section for resulting nomenclatural problems). He argued that the inner rows are certainly not ventral rows, because they do not show a (zigzagging) midventral pattern. Later, he distanced oneself from this proposal and accepted both *Perisincirra* and *Engelmanniella* (Foissner 1984, p. 119). *Engelmanniella mobilis* has parental marginal rows with widely spaced cirri whereas the cirri of all rows are (primarily) widely spaced in *Perisincirra*. In addition, *Engelmanniella* lacks caudal cirri, which are (very likely) present in *Perisincirra*. Probably there are further significant differences between these two genera, for example, in morphogenesis and ultrastructure (e.g., Wirnsberger-Aescht et al. 1989); however, relevant data are lacking for the present genus. Anyhow, a synonymy of *Perisincirra* and *Engelmanniella* can be excluded.

Curds et al. (1983, p. 420) again synonymised *Perisincirra* with *Uroleptus* obviously ignoring the apparent differences in the cirral pattern (zigzagging midventral pattern lacking vs. present).

Morphology: Body length 85–160 µm, on average 115 µm, width about 7–12 µm; length:width ratio about 10:1, sometimes up to 15:1; impregnated specimen illustrated circa 14:1 (Fig. 81a; all measurements after fixation). Body outline filiform,

[1] Jankowski (1979, p. 61) wrote: "*Perisincirra* Jk., 1978. TB *Uroleptus kahli* Grolière, 1975 (*Uroleptopsis kahli*, ibidem)".

that is, very slender with parallel margins and narrowly rounded ends. Body very flexible. Two very slender elongate (only 2 µm wide!) macronuclear nodules in left body half, connected by fine thread; one globular micronucleus attached to each macronuclear nodule. Contractile vacuole, details about cytoplasm, cortical granules, and movement neither mentioned nor illustrated.

Adoral zone inconspicuous because occupying only 16% of body length on average, formed like a question mark according to Fig. 81a, almost gonostomatid according to a photomicrograph in Grolière (1975, his Fig. 10), composed of 18–20 membranelles. Buccal field very narrow. Paroral about 8–10 µm long, commences behind buccal cirrus; endoral not described, likely very difficult to recognise due to narrow buccal cavity. Pharyngeal fibres extend far posteriorly (Fig. 81a).

Cirral pattern conspicuous due to widely spaced cirri (Fig. 81a). Three frontal cirri close to anterior end; one buccal cirrus ahead of paroral. Arrangement/number of cirri on frontal field not exactly recognisable (Fig. 81a). Further details about cirri on frontal field, see Fig. 81a. Each two cirral rows right and left of midline. Frontoterminal(?), postoral ventral, pretransverse ventral, and transverse cirri lacking. Length of cirri about 6 µm (estimated from Fig. 81a, perhaps not correctly illustrated).

Dorsal bristles short (likely around 3 µm), arranged in three (bipolar?) kineties. Caudal cirri neither mentioned nor illustrated. Since the cirral pattern of such slender hypotrichs is very difficult to recognise in every detail, it cannot be excluded that Grolière has overlooked them or misinterpreted as marginal/ventral cirri. No illustration of dorsal side provided.

Occurrence and ecology: Type locality of *Perisincirra kahli* is the area Landie and Plaine Jacqueau (Auvergne, France), where Grolière (1975) found it in the "mare de Pisseport" on the mountainside of the volcano Montchalm in November 1973 (Grolière 1975; 1977, p. 349). Cultures grew very well at 5 °C. Record

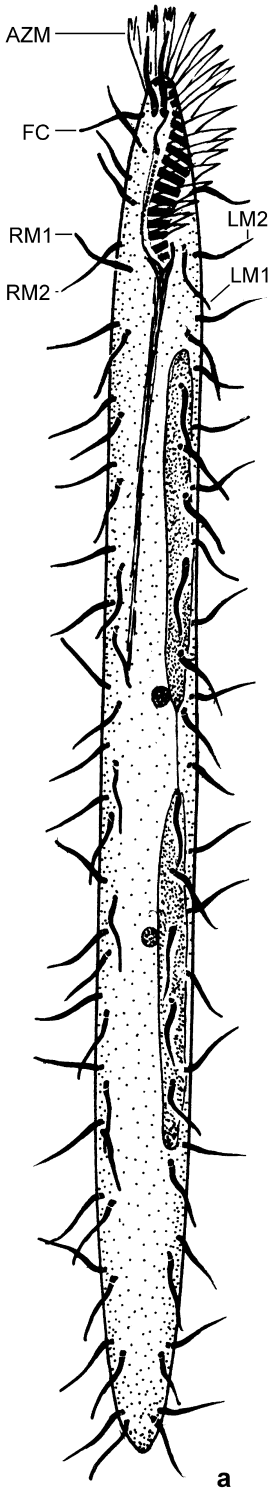


Fig. 81a *Perisincirra kahli* (from Grolière 1975. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus, 135 µm. AZM = distal end of adoral zone of membranelles, FC = right frontal cirrus, LM1, 2 = inner (1) and outer (2) left cirral row, RM1, 2 = inner (1) and outer (2) right cirral row. Page 471.

not substantiated by morphological data: wet mosses in Slovenský raj in the Stratenská hornatin highland, Slovakia (Tirjaková & Matis 1987, p. 11). The record of "*Uroleptus kahli*" from Antarctic soil in Sudzuki (1979, p. 124) likely refers to the homonym described by Buitkamp (1977; now *Hemisincirra buitkampi*; for review, see Berger 2008, p. 393) because in the reference section only the paper by Buitkamp is cited. Food not known.

Perisincirra paucicirrata Foissner, Agatha & Berger, 2002
(Fig. 82a–g, Table 25)

2002 ***Perisincirra paucicirrata* nov. spec.**[1] – Foissner, Agatha & Berger, Denisia, 5: 628, Fig. 140a–g, Table 125 (Fig. 82a–g; original description; the holotype slide [accession number 2002/726] and three paratype slides [2002/727–729] as well as three voucher slides [2002/730–732] have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Foissner et al. 2002a, p. 41, Aescht 2008, p. 172).

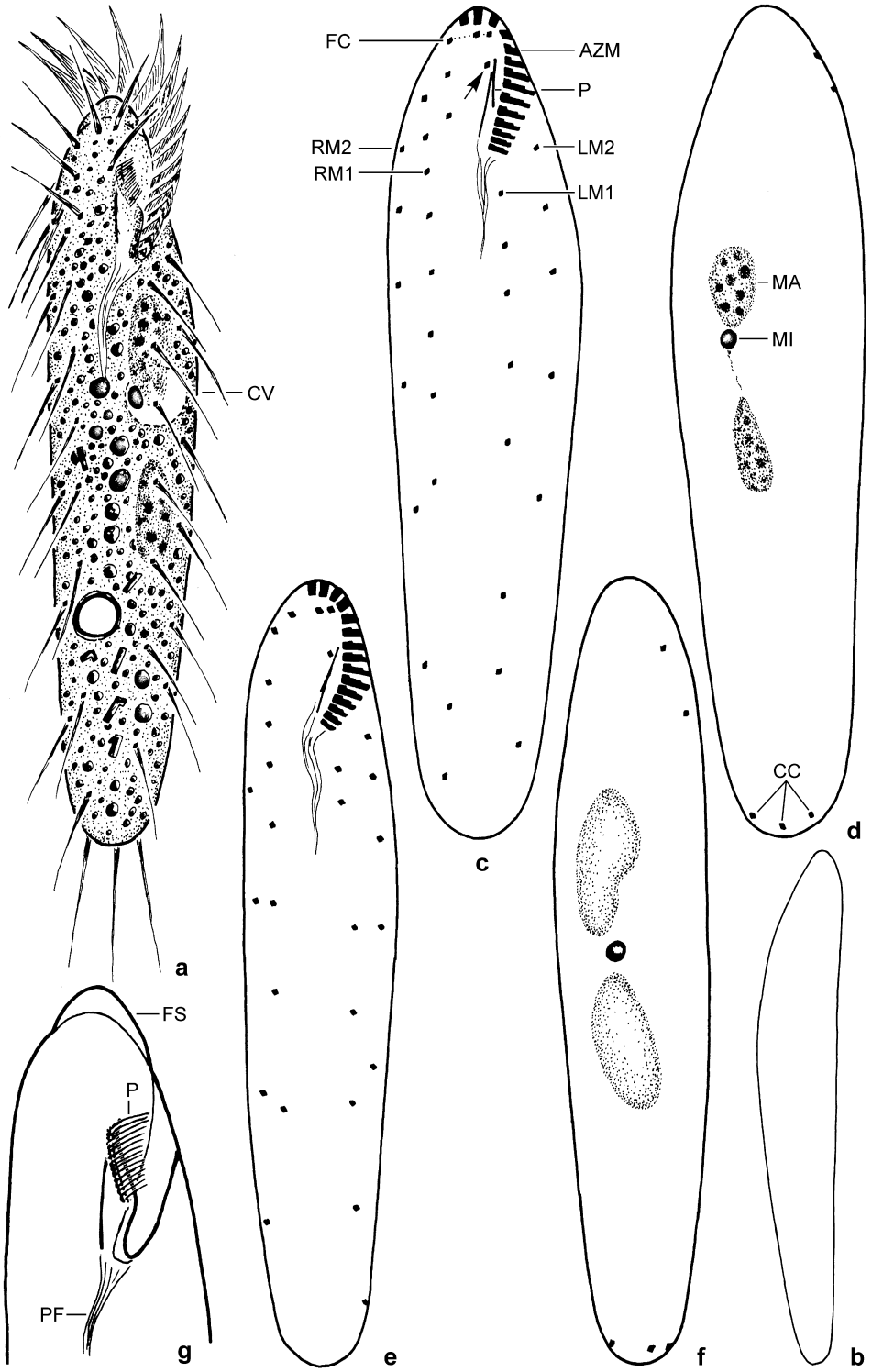
Nomenclature: The species-group name *paucicirrata* is a composite of the Latin adjectives *paucus* (few, small, slight) and *cirratus* (hairy), referring to the few, widely spaced cirri (Foissner et al. 2002a).

Remarks: This species is very likely congeneric with the type species as indicated by the same number of cirral rows bearing fine, widely spaced cirri, the slender shape, the short adoral zone (less than 20% of body length on average), the two macronuclear nodules, and the three dorsal kineties. Grolière (1975) did not mention caudal cirri; perhaps he misinterpreted the posteriormost cirri as ventral/marginal cirri because the infraciliature of such slender and fragile species is very difficult to analyse.

Perisincirra paucicirrata differs from *P. kahli* in body length (64–121 µm, on average 85 µm vs. 85–160 µm, on average 115 µm in protargol preparations),

Fig. 82a–g *Perisincirra paucicirrata* (from Foissner et al. 2002a. a, b, g, from life; c–f, protargol impregnation). **a:** Ventral view of a representative specimen, 108 µm. **b:** Right lateral view. **c, d:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 87 µm. Arrow marks buccal cirrus; frontal cirri connected by dotted line. This specimen has two parabuccal cirri behind the right frontal cirrus. The dorsal kineties (likely three) could not be recognised unequivocally and are thus not shown (see text). **e, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of two Namibian specimens (about 80 µm), which sometimes lack cirri behind the right frontal cirrus. **g:** Oral apparatus showing paroral on buccal lip and paroral cilia decreasing in length from anterior to posterior. AZM = adoral zone of membranelles, CC = caudal cirri, CV = contractile vacuole, FC = right frontal cirrus, FS = frontal scutum, LM1, 2 = inner (1) and outer (2) left cirral row, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RM1, 2 = inner (1) and outer (2) right cirral row. Page 474. →

[1] Foissner et al. (2002) provided the following diagnosis: Size about 100 × 20 µm in vivo; elongate ellipsoidal. 2 macronuclear nodules and 1 micronucleus in between. On average 15 adoral membranelles, 9 cirri in right (marginal?) row one, and 6 in row two, 7 in left row one and 6 in row two, 1 buccal cirrus, and 2 cirri behind right frontal cirrus. 3 dorsal kineties with a caudal cirrus each.


CV
a
FC
AZM
P
RM2
RM1
LM2
LM1
c
MA
MI
CC
d
e
f
b
FS
P
PF
g

length:width ratio (in protargol preparations on average 4.1:1 vs. 10:1), the lower number of adoral membranelles (13–17 vs. 18–20), and the lower number of cirri per row (3–12 vs. 16–20). In addition, the type population of *P. paucicirrata* usually has two cirri behind the right frontal cirrus whereas parabuccal cirri are likely lacking in *P. kahli*, but also in *P. paucicirrata* specimens from Namibia (Fig. 82e). *Perisincirra longicirrata* has six cirral rows (vs. 4 in congeners) and a much more conspicuous oral apparatus because of the higher number of adoral membranelles (21 vs. 15) and the deeper and wider buccal cavity.

In vivo, the present species is thus recognisable by the following combination of features: long, fine, widely spaced cirri; small size (around 100 × 20 µm); two macronuclear nodules. Of course the identification should be checked in protargol preparations because there are likely several other, yet undescribed species in *Perisincirra* and similar genera (Foissner et al. 2002a).

Morphology: The following description is based on the type material from Australia only. Some deviating data from the Namibian site (64) population are added at the end.

Body size 70–130 × 15–30 µm, usually 90–110 µm long in vivo, length:width ratio about 5:1 in vivo and 2.2–8.6:1, on average 4.1:1 in protargol preparations. Body outline elongate ellipsoidal with margins slightly converging posteriorly. Body very flexible, but acontractile; only slightly flattened dorsoventrally (Fig. 82a–c, Table 25). Macronuclear nodules left of midline in middle body third, usually elongate ellipsoidal, rarely ellipsoidal or even globular; chromatin bodies small to large. Micronucleus only about 3 × 2 µm in vivo and thus difficult to recognise both in life and in protargol preparations, usually one near at posterior end of anterior macronuclear nodules and thus more or less distinctly between the two beads (Fig. 82a, d). Contractile vacuole without conspicuous collecting canals, distinctly ahead of mid-body at left cell margin. Cortical granules lacking. Cytoplasm colourless, usually packed with highly refractive fat globules 0.5–3.0 µm across making cells dark under low magnification (40–100×) and bright field illumination; in posterior body portion usually some ordinary crystals. Swims and glides rather rapidly on microscope slide and debris, showing great flexibility.

Adoral zone of usual shape and structure, conspicuously short, that is, occupying only 11–25%, on average 18% of body length, composed of an average of 15 membranelles about 5 µm wide in vivo and of ordinary structure (Fig. 82a, c, g, Table 25). Buccal cavity flat and narrow, right margin forms convex lip partially covering proximal portion of adoral zone and bearing paroral composed of a 5–6 µm long, straight series of cilia decreasing in length from 5 µm anteriorly to 3 µm posteriorly; endoral also more or less straight, but slightly longer than paroral, with which it forms an acute angle. Pharyngeal fibres inconspicuous, extend straight backwards.

Cirral pattern rather constant, while number of cirri within rows highly variable (Fig. 82a, c, Table 25). All cirri rather long and conspicuously fine, that is, about 15 µm and composed of only 2–4 cilia. Frontal cirri in transverse pseudorow, of about same size as other cirri. Buccal cirrus right of anterior end of paroral and ahead of

endoral. Usually two, rarely three cirri or only one cirrus behind right frontal cirrus. Frontoterminal, postoral ventral, pretransverse ventral, and transverse cirri lacking. Invariably two rows of conspicuously widely spaced (marginal?) cirri both right and left of midline.

Dorsal bristles about 4 µm long in life, arranged in (very likely) three sparsely ciliated rows each terminating with an about 22 µm long, fine caudal cirrus (Fig. 82d). Unfortunately, the dorsal kineties could not be recognised unequivocally and are thus not shown in the illustrations.

Namibian site (64) population: The specimens from the Etosha National Park are highly similar to the Australian type material, but have only one (vs. two), rarely none (Fig. 82e) cirrus (= parabuccal cirrus) behind the right frontal cirrus. Furthermore, 20% of the cells have two micronuclei (against one in type population).

Occurrence and ecology: *Perisincirra paucicirrata* likely prefers semiterrestrial habitats. Type locality is the bank of the Shoalhaven River near the village of Bungonia (35°S 149°E; Australia), where it was discovered in mud from rock-pools (Foissner et al. 2002a). In addition, it was isolated from two sites in Namibia: (i) Site (64)[1], Aus waterhole (19°10'S 16°10'E) in the Etosha National Park; waterhole dry and overgrown with grasses; material collected was litter, roots, and soil from 0–5 cm in central area of water hole, pH 6.3, slightly saline (5‰). (ii) Site (70), Okerfontein waterhole (18°45'S 16°45'E) in the Etosha National Park; salt-bush (*Suaeda* spp.) and grass (*Sporobolus* spp.) girdle near the toilet; material collected was litter with cyanobacteria crusts, roots, and soil up to 5 cm depth, pH 8.4, saline (15‰). Further details on Namibian sites, see Foissner et al. (2002a, p. 28, 30). *Perisincirra paucicirrata* feeds on fungal spores and hyphae (Foissner et al. 2002a).

Perisincirra longicirrata Foissner, Agatha & Berger, 2002
(Fig. 83a–e, Table 25)

2002 ***Perisincirra longicirrata* nov. spec.**[2] – Foissner, Agatha & Berger, Denisia, 5: 632, Fig. 141a–e, Table 125 (Fig. 83a–e; original description; the holotype slide [accession number 2002/548] and two paratype slides [2002/549, 550] have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Foissner et al. 2002a, p. 41 and Aescht 2008, p. 163).

Nomenclature: The species-group name *longicirrat·us*, *-a*, *-um* (adjective [m; f; n]) is a composite of the Latin adjectives *longus* (long) and *cirratus* (hairy), alluding to the long cirri (Foissner et al. 2002a).

[1] In Table 1 of the original description we erroneously wrote that *P. paucicirrata* occurred in Namibian site (63) (Foissner et al. 2002a, p. 41).

[2] Foissner et al. (2002a) provided the following diagnosis: Size about 80 × 30 µm in vivo; elongate ellipsoidal to bluntly fusiform. 2 macronuclear nodules with a micronucleus each. On average 21 adoral membranelles, about 12 cirri each in three (marginal?) rows right of midline and about 8 cirri each in the three rows left of midline, 1 buccal cirrus, 1 cirrus behind right frontal cirrus, and 3 caudal cirri. Cirri widely spaced and fine, but up to 30 µm long.

Remarks: The rows of widely spaced, long and fine cirri as well as the caudal cirri indicate a closely relationship with *P. paucicirrata*. It differs from both congeners in body shape (body length:width ratio 2.8:1 vs. 4.1–10.0:1), number of cirral rows (6 vs. 4), and the much deeper and wider buccal cavity making the oral apparatus rather conspicuous (vs. inconspicuous).

Perisincirra longicirrata is reminiscent of *Kahliella* spp. (p. 347) because of the increased number of cirral rows and the adoral zone, which is more or less gonostomatid in both groups. However, *Kahliella* species have narrowly spaced cirri in at least two of the rows and a different caudal cirri pattern (many cirri on one kinety). *Neogeneia hortualis* has also rather widely spaced cirri in most rows, but possesses a distinctly higher number of cirral rows (11–13 vs. 6), only two dorsal kineties (vs. 4), and only one caudal cirrus against three (p. 483). *Parastrongylidium* species, which also have a rather similar size and overall appearance, posses a moniliform macronucleus, more cirral rows (11–13 vs. 6) and cirri per row, one dorsal kinety, and lack caudal cirri (e.g., Aescht & Foissner 1992). In life, *Perisincirra longicirrata* is recognisable by the following combination of features: small size (100 µm or less), rather conspicuous buccal cavity, and, most important, the six rows of very long, fine, and widely spaced cirri. Identifications should be checked by protargol impregnation because there are several, as yet undescribed similar species, and slender specimens are easily confused with wide individuals of *P. paucicirrata* (Foissner et al. 2002a).

Morphology: Body size 60–100 × 20–40 µm in life, usually around 80 × 30 µm; length:width ratio about 2.8:1 in life and 1.8–2.6:1, on average 2.2:1 in protargol preparations, where specimens are usually slightly inflated. Body outline elongate elliptical to bluntly fusiform with anterior region slightly more narrowed than indistinctly pointed posterior portion. Body very flexible, but acontractile; only slightly flattened dorsoventrally (Fig. 83a–c, Table 25). Macronuclear nodules left of midline in central quarters of cell, usually ellipsoidal, rarely almost globular or elongate ellipsoidal; chromatin bodies small and globular. Usually one spherical, compact micronucleus attached to each macronuclear nodule at various positions. Contractile vacuole without distinct collecting canals near mid-body at left cell margin. Cortical granules lacking. Cytoplasm colourless, usually packed with highly refractive fat globules 1–6 µm across, except in buccal field, making cells dark under low magnification and bright field illumination; crystals sparse or lacking. Rotates and glides rather rapidly on microscope slide and debris showing great flexibility.

Oral apparatus gonostomatid, that is, adoral zone extends straight along left anterior body margin, performing right bend and slight clockwise rotation to plunge into buccal cavity slightly ahead of mid-body. Adoral zone occupies 29–44%, on average 37% of body length, composed of an average of 21 membranelles with bases of largest membranelles up to 5 µm wide and of ordinary fine structure (Fig. 83a, d). Buccal cavity rather deep and wide and conspicuously soft; right margin without lip, distinctly curved, extends from left end of frontal scutum to near proximal end of adoral zone. Paroral on right margin of buccal cavity, almost straight or slightly

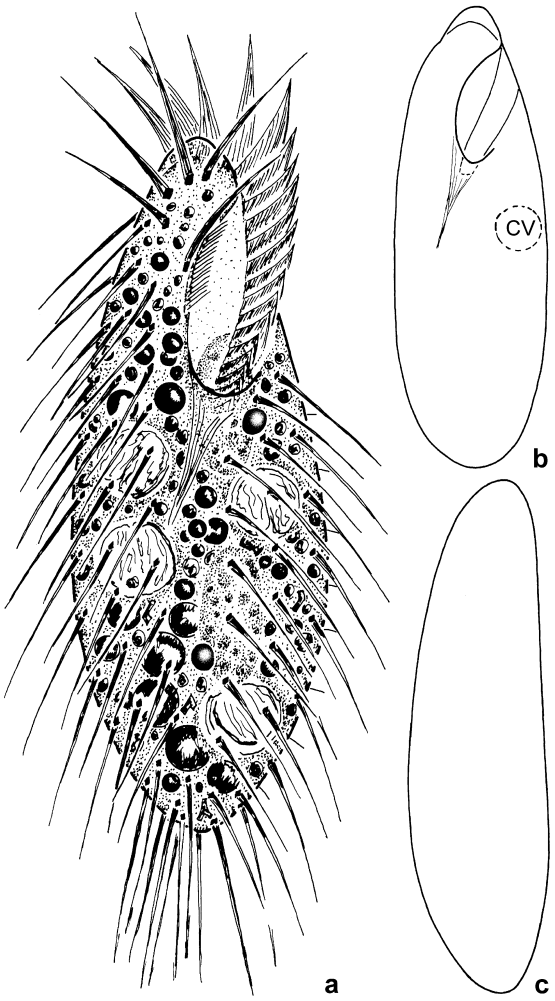


Fig. 83a–c *Perisincirra longicirrata* (from Foissner et al. 2002a. From life). **a:** Ventral view of a representative, bluntly fusiform specimen, 82 µm. **b:** Ventral view of an elliptical specimen showing the contractile vacuole and the wide buccal field, a distinct difference to the congeners. **c:** Lateral view showing that *P. longicirrata* is only slightly flattened dorsoventrally. CV = contractile vacuole. Page 477.

curved, composed of an 8 µm long series of about 20, in life circa 5 µm long cilia. Endoral about 10 µm long, begins about 4 µm ahead of paroral and extends to mid of buccal cavity. Pharyngeal fibres extend obliquely backwards.

Cirral pattern rather constant, while number of cirri within rows highly variable (Fig. 83a, d, Table 25). Frontal cirri 20–30 µm long in life and composed of up to 3 × 4 basal bodies, that is, slightly longer and distinctly larger than other cirri, which are 15–25 µm (posteriorly also up to 30 µm) long and likely composed of 2 × 2 or 2 × 3 basal bodies only. Buccal cirrus ahead of endoral and slightly behind anterior end of paroral. Invariably one cirrus (= parabuccal cirrus) behind right frontal cirrus. Frontoterminal, postoral ventral, pretransverse ventral, and transverse cirri lacking. Invariably three posteriorly more or less distinctly curved rows of conspicuously widely spaced cirri both right and left of midline.

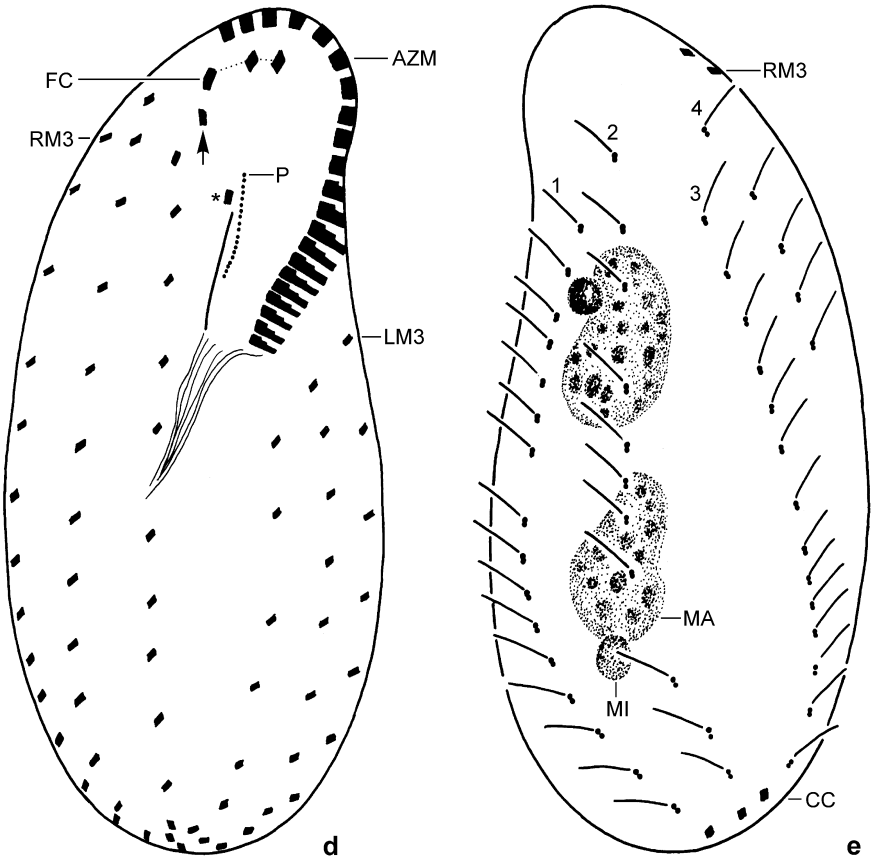


Fig. 83d, e *Perisincirra longicirrata* (from Foissner et al. 2002a. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 67 µm. Dotted line connects frontal cirri. Arrow denotes cirrus behind right frontal cirrus (= parabuccal cirrus, = cirrus III/2), asterisk marks buccal cirrus. AZM = adoral zone of membranelles, CC = caudal cirri on dorsal kineties 1–3, FC = right frontal cirrus, LM3 = outermost cirral row in left body half, MA = macronuclear nodule, MI = micronucleus, P = paroral, RM3 = outermost cirral row in right body half, 1–4 = dorsal kineties (kinety 4 is probably a dorsomarginal kinety; see text). Page 477.

Dorsal bristles about 5 µm long in life, arranged in four kineties (Fig. 83e). All rows more or less distinctly shortened anteriorly, rows 1–3 each terminating with a 20–30 µm long caudal cirrus; kinety 4 likely a dorsomarginal kinety because ending ahead of mid-body and without caudal cirrus (see remarks).

Occurrence and ecology: To date only found at two sites in Africa. Type locality of *Perisincirra longicirrata* is the University Campus in Abomey-Calavi (06°27'N 02°21'E), Benin, where we discovered it in red, hard, sandy soil (pH 7.3) with some litter and roots (Foissner et al. 2002a). In addition, it occurred in Namibian site (73), the Daan Viloen Game Park in Windhoek (22°35'S 17°05'E; Foissner et al. 2002a, p.

30). The sample was dry and moist mud from pools (pH 6.2) from granitic rocks in a stream below the dam. The material was collected on 04.03.1994 and investigated on 02.08.1999, that is, cysts outlive 5.5 years. At both sites, *Perisincirra longicirrata* was rare. Feeds on about 10 × 6 µm-sized, heterotrophic flagellates (*Polytoma* sp.; Foissner et al. 2002a).

Neogeneia Eigner, 1995

1995 ***Neogeneia* nov. gen.**[1] – Eigner, Europ. J. Protistol., 31: 348 (original description). Type species (by original designation): *Neogeneia hortualis* Eigner, 1995.
2001 ***Neogeneia* Eigner 1995** – Aescht, Denisia, 1: 105 (catalogue of generic names of ciliates).
2001 ***Neogeneia* Eigner, 1995** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 48 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Neogeneia* Eigner, 1995**[2] – Lynn & Small, Ciliophora, p. 455 (guide to ciliate genera).
2007 ***Neogeneia* Eigner, 1995** – Jankowski, Ciliophora, p. 462 (revision of ciliates).
2008 ***Neogeneia* Eigner, 1995** – Lynn, Ciliated protozoa, p. 357 (revision of ciliates).

Nomenclature: According to Eigner (1995), *Neogeneia* (Greek) means newly developed because there are "many neokinetal developments during divisional morphogenesis"; for detailed explanation of this concept, see Eigner (1995, 1997). Feminine gender (Eigner 1995; Aescht 2001, p. 290).

Characterisation (A = supposed apomorphy): Kahliellidae(?). Body circular or elliptical in cross section, that is, not distinctly flattened dorsoventrally (A?). Adoral zone of membranelles formed like a question mark. Undulating membranes relatively short, almost straight, not intersecting. Three slightly enlarged frontal cirri. Usually one buccal cirrus. Two or three frontoventral rows extending at least to midbody. Transverse cirri lacking. Two or more left marginal rows and one or more right marginal rows. Two (type) or three (*N. costata*; uncertain) bipolar dorsal kineties. Anterior portion of rightmost right marginal row composed of dorsal bristles, perhaps an early or vestigial dorsomarginal kinety. Dorsal kinety fragmentation lacking. Caudal cirri present. Anlagen I–III of opisthe originate from oral primordium. Rightmost (outermost) right marginal row originates (very likely) de novo and anlagen of remaining right marginal rows originate in right abutting rows (A). Parental right marginal rows retained in postdividers. Left marginal rows composed of new (anterior portion) and parental (posterior portion) cirri (A). Terrestrial and limnetic(?).

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[1] Eigner (1995) provided the following diagnosis: Elliptical Kahliellidae with more than one long cirral row on right and left side of body. At least two of them are typically parental (old) on right side (distinctly shorter than a neighboring cirral row and contain usually wider spaced and enlarged cirri). Parental cirri also in posterior half of cirral rows on left side. Caudal cirrus. Combined cirral row develops neokinetally during morphogenesis. Neokinetal wave to the left on right side and from anterior to posterior on left side of adoral membranelles.

[2] Lynn & Small (2002) provided the following characterisation: Ventral cirri not obviously in files, but visible during morphogenesis; at least one rightmost ventral cirral file of parental origin and several posterior leftmost cirri of left cirral file of parental origin; transverse cirri, absent; caudal cirri, absent.

Additional characters: Body length around 100 µm. Body outline elliptical to elongate elliptical. Body rather stiff. Two macronuclear nodules. Contractile vacuole about in mid-body near left body margin. Cirri within rows rather widely spaced, fine.

Remarks: Eigner (1995) found a species resembling *Kahliella* sp. Because of distinct differences in cell division, he fixed it as type species of a new genus, *Neogeneia*. Indeed, some ontogenetic details are highly specific so that the validity of *Neogeneia* is beyond doubt. Whether or not the assignment of *Kahlia costata* Kahl, 1932 to *Neogeneia* by Eigner (1995) is correct has to be checked by a detailed redescription and ontogenetic data.

Eigner (1995) established *Neogeneia* in the Kahliellidae because it has more than one longitudinal cirral row on the right side of the body and neokinetal anlagen development. Somewhat later, he eliminated the kahliellids and put the present genus into the Parakahliellidae (see next paragraph). By contrast, Lynn & Small (2002), Berger (2007a), Jankowski (2007), and Lynn (2008) accepted the original classification, obviously simply because parental cirri are retained after division. I preliminary assent to this view, inter alia, because I have no better idea how to interpret the data. I recommend that molecular data of a reliably identified population should be awaited before a new assignment is proposed. Due to the lack of a dorsal kinety fragmentation I strongly suppose that *Neogeneia* is not an oxytrichid. Whether or not it belongs to the Dorsomarginalia (hypotrichs with a dorsomarginal kinety) is not appreciable according to the present knowledge because the relevant feature has an intermediate status in *Neogeneia*, that is, some dorsal bristles are ahead of the outermost right marginal row, but do not separate and migrate onto the dorsal side. Perhaps one of the two already existing classifications (Kahliellidae, Parakahliellidae) will be confirmed.

Neogeneia was classified in the Parakahliellidae by Eigner (1997, 1999), inter alia, because of the neokinetal 1 anlagen formation and the lack of long primary primordia (Eigner 1997, p. 555). According to Eigner (1997, p. 563), *Neogeneia hortualis* is the supposed ancestor[1] of the Parakahliellidae, inter alia, because the dorsomarginal kinety (= anterior portion of right marginal row 3; Fig. 84c, l) is not yet displaced onto the dorsal side, that is, Eigner (1997) considered this part of the row as progenitor of the dorsomarginal kinety.

Neogeneia differs from *Kahliella* (p. 347), inter alia, in the lack of a distinct dorsomarginal kinety (vs. present) and the shape of the adoral zone of membranelles (more or less shaped like a question mark vs. gonostomatid). Further, they differ in the number of frontoventral rows/anlagen (5 vs. 6) and the position of the combined row (anterior portion composed of dorsal bristles, rear portion consisting of cirri; Eigner 1995, p. 343), namely on the right body side (Fig. 84c) against on the left side (Fig. 65g). Perhaps the anterior bristle portion is a vestigial dorsomarginal kinety.

[1] For detailed discussion of the survival of stem species, see Ax (1984, p. 73).

In *Deviata*, the second genus described by Eigner (1995), the cirri are rather narrowly spaced, inter alia, because no parental cirri are retained after cell division (p. 555). The rather widely spaced cirri within the individual rows of *Neogeneia* are reminiscent of *Perisincirra* (p. 463). However, these species have less cirral rows.

Species included in *Neogeneia* (alphabetically arranged basionyms are given): (1) *Kahlia costata* Kahl, 1932; (2) *Neogeneia hortualis* Eigner, 1995 (type species).

Key to *Neogeneia* species

Identification of *Neogeneia* species requires both live observation (cortical ribs, defecation vacuole) and protargol impregnation (number of long cirral rows). Perhaps the number of dorsal kineties is also different (2 in *N. hortualis* vs. 3 in *N. costata*). However, the value for *N. costata* is not yet confirmed by silver impregnation. If you cannot identify your specimen/population with the key below, see also *Kahliella* (p. 347), *Deviata* (p. 555), or *Perisincirra* (p. 463).

1 Macronuclear nodules sausage-shaped; about 13 long cirral rows; longitudinal ribs lacking; conspicuous defecation vacuole in rear body portion lacking (Fig. 84a–c). . . . . *Neogeneia hortualis* (p. 483)

\- Macronuclear nodules ellipsoidal; about 7 long cirral rows; longitudinal ribs present; conspicuous defecation vacuole in posterior body portion present (Fig. 85a, b). . . . . *Neogeneia costata* (p. 494)

Neogeneia hortualis Eigner, 1995

(Fig. 84a–n, Tables 26, 27)

1995 ***Neogeneia hortualis* nov. spec.**[1] – Eigner, Europ. J. Protistol., 31: 349, Fig. 17–28, Table 2 (Fig. 84a–n; original description; the slide [accession number: 1994/86][2] containing the holotype specimen [marked] and several paratype specimens is deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Aescht 2003, p. 388; 2008, p. 159).

1997 ***Neogeneia hortualis* Eigner, 1995** – Eigner, J. Euk. Microbiol., 44: 563, Fig. 23 (Fig. 84b, c; diagrammatic representation of cirral pattern and ontogenesis).

2001 ***Neogeneia hortualis* Eigner, 1995** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 48 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2002 ***Neogeneia hortualis*** – Lynn & Small, Ciliophora, p. 455, Fig. 43A, B (Fig. 84b, c; guide to ciliate genera).

Nomenclature: The species-group name *hortualis* (from the Latin *hortensis*; belonging to the garden) refers to the fact that the species was discovered in a compost heap

[1] Eigner (1995) provided the following diagnosis: Body slightly flattened. Size in vivo 70–90 × 25–35 µm. 3 enlarged cirri in frontal field. 8 long cirral rows right of adoral zone of membranelles, 2 of which are typically parental. 3–5 long cirral rows left of adoral zone of membranelles. 2 large connected macronuclear nodules. 2 long dorsal kineties, single caudal cirrus.

[2] According to Eigner (1995, p. 349), the accession number is 94/4.

Table 26 Designation of cirral rows and anlagen in *Neogeneia hortualis* in present book and in original description (Eigner 1995)

Present book (abbreviation)	Eigner (1995)	Structures formed and/or remarks
Cirral row I; anlage I (I)	Cirral row I1; anlage 1	Left frontal cirrus (I/1)
Cirral row II; anlage II (II)	Cirral row I2; anlage 2	Middle frontal cirrus (II/3) and buccal cirrus (II/2)
Cirral row III; anlage III (III)	Cirral row I3; anlage 3	Right frontal cirrus (III/3) and parabuccal cirri. First long cirral row (III) right of adoral zone.
Cirral row IV; anlage IV (IV)	Cirral row I4; anlage 4	Anlage IV is formed within parental row IV
Cirral row V; anlage V (V)	Cirral row I5; anlage 5	Anlage V of proter is formed within parental row V; anlage V of opisthe is formed de novo (Fig. 84g)
Inner parental row (P2)	Old cirral row P2 (fifth generation)	This is the grandparental right marginal row 1
Outer parental row (P1)	Old cirral row P1 (fourth generation)	This is the parental right marginal row 1
Right marginal row 1 (RMR1); for anlage, see last column	Cirral row I6; anlage 6	Anlage for RMR1 is formed within RMR2. Retained in next generation, that is, forms then P1
Right marginal row 2 (RMR2); for anlage, see last column	Cirral row I7; anlage 7	Anlage for RMR3 is formed within RMR3
Right marginal row 3 (RMR3); for anlage, see last column	Cirral row I8; anlage 8 (neokinetal)	Originates more or less de novo left of anlage for RMR2. Anteriormost portion composed of basal body pairs, reminiscent of a dorsomarginal kinety
Left marginal row 1 (LMR1); for anlage, see last column	Cirral row IL1 + PL1	Consists of new (anterior portion; formed by within anlage) and parental (posterior portion) cirri (Fig. 84d).
Left marginal row 2 (LMR2); for anlage, see last column	Cirral row IL2 + PL2	See previous entry
Left marginal row 3 (LMR3); for anlage, see last column	Cirral row IL3 + PL3	See previous entry
Left marginal row 4 (LMR4); for anlage, see last column	Cirral row IL4 + PL4	See previous entry
Left marginal row 5 (LMR5); for anlage, see last column	Cirral row IL5 + PL5	See previous entry

Table 27 Morphometric data on *Neogeneia hortualis* (from Eigner 1995)

Characteristics [a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length [d]	77.7	78.0	4.9	–	6.4	58.0	84.0	15
Body, width	25.6	24.0	2.7	–	10.7	22.0	32.0	15
Adoral zone of membranelles, length	23.7	24.0	1.9	–	7.9	20.0	27.0	15
Anterior macronuclear nodule, length	20.7	22.0	3.7	–	17.8	16.0	26.0	15
Anterior macronuclear nodule, width	5.9	6.0	1.5	–	25.5	3.0	8.0	15
Posterior macronuclear nodule, length	31.0	33.0	4.0	–	12.9	28.0	38.0	15
Posterior macronuclear nodule, width	4.3	4.0	0.6	–	13.8	3.0	5.0	15
Macronuclear nodules, number	2.0	2.0	0.0	–	0.0	2.0	2.0	15
Adoral membranelles, number	22.7	22.0	1.2	–	5.4	20.0	24.0	15
Frontal cirri, number	3.0	3.0	0.0	–	0.0	3.0	3.0	15
Buccal cirri, number	1.0	1.0	0.0	–	0.0	1.0	1.0	15
Long cirral rows right of adoral zone, number [b, c]	8.0	8.0	0.0	–	0.0	8.0	8.0	15
Cirral row/anlage I, number of cirri [c]	1.0	1.0	0.0	–	0.0	1.0	1.0	15
Cirral row/anlage II, number of cirri [c]	2.0	2.0	0.0	–	0.0	2.0	2.0	15
Cirral row/anlage III, number of cirri [c]	11.1	11.0	1.0	–	9.3	9.0	13.0	15
Cirral row/anlage IV, number of cirri [c]	11.1	11.0	1.3	–	11.5	8.0	13.0	15
Cirral row/anlage V, number of cirri [c]	17.1	17.0	1.3	–	7.4	15.0	19.0	15
Inner parental row, number of cirri [c]	3.0	3.0	–	–	–	2.0	4.0	15
Outer parental row, number of cirri [c]	8.8	8.5	0.8	–	9.0	8.0	10.0	10
Inner right marginal row, number of cirri [c]	20.2	21.0	2.5	–	12.2	14.0	24.0	15
Middle right marginal row, number of cirri [c]	18.3	18.0	1.8	–	9.6	16.0	21.0	15
Outer right marginal row, number of cirri [c]	13.5	13.0	2.3	–	16.8	12.0	19.0	15
Left marginal row 1, number of cirri [c]	9.7	10.0	1.5	–	15.4	7.0	12.0	15
Left marginal row 2, number of cirri [c]	9.6	10.0	1.7	–	18.0	6.0	14.0	15
Left marginal row 3, number of cirri [c]	12.7	13.0	2.8	–	22.6	8.0	15.0	15
Left marginal row 4, number of cirri [c]	14.4	15.0	1.6	–	11.2	12.0	15.0	7
Left marginal row 5, number of cirri [c]	13.0	13.0	–	–	–	13.0	13.0	1
Dorsal kineties, number	2.0	2.0	0.0	–	0.0	2.0	2.0	15
Caudal cirri, number	1.0	1.0	0.0	–	0.0	1.0	1.0	15

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] Long cirral rows have their posterior end behind the level of the buccal vertex.

[c] For designation of cirral rows in original description (Eigner 1995), see Table 26.

[d] Note that the specimen illustrated in Fig. 84b, c is about 97 µm long according to the scale bar. This value is distinctly above the maximum value (84 µm) mentioned in the table. Three possibilities exist: (i) the scale bar is incorrect; (ii) the maximum value in the table is a printers error; (iii) the specimen illustrated is not considered in the morphometry. Supposed that the specimen in Fig. 84b, c is indeed 97 µm long, the body size is unsuitable for separation of *N. hortualis* and *N. costata* as suggested by Eigner (1995).

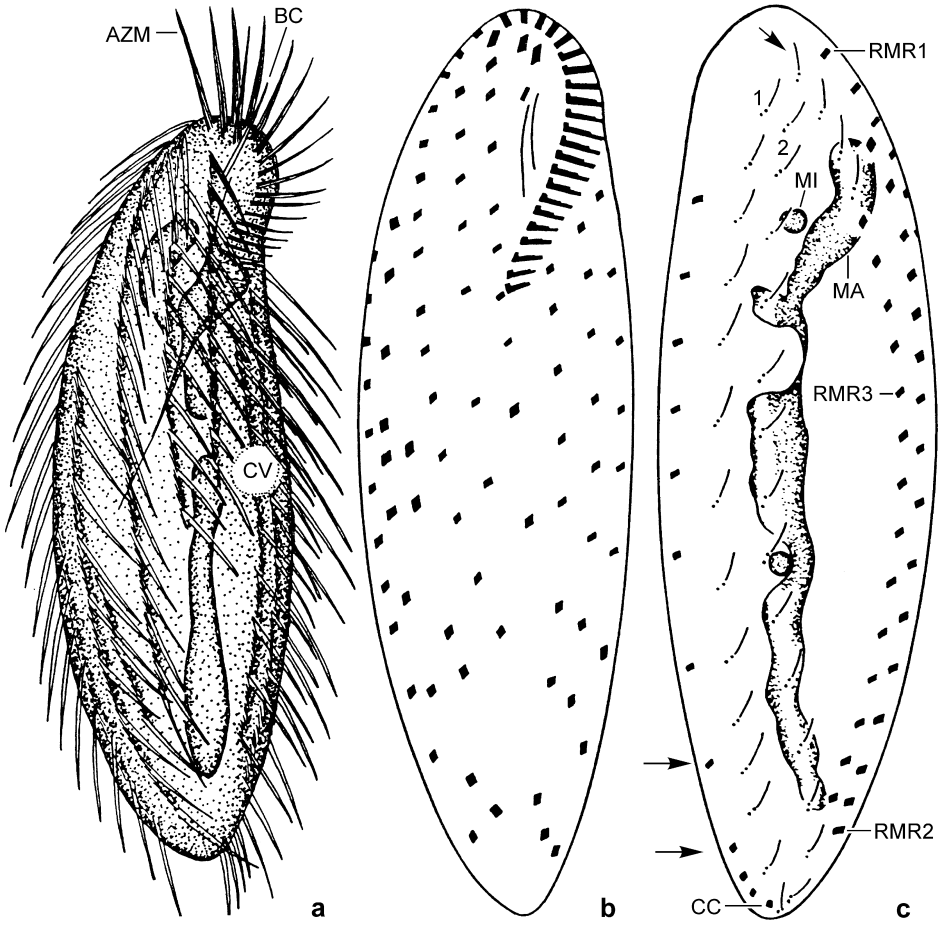

Fig. 84a–c *Neogeneia hortualis* (from Eigner 1995. a, from life; b, c, protargol impregnation). **a:** Ventral view, 82 µm. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of same(?) specimen, 97 µm (see footnote d of Table 27). The oblique arrow marks the dorsal bristles ahead of the outermost right marginal row (see text). The horizontal arrows mark the border between the new (anterior) and parental (posterior) portion of the outermost left marginal row. For detailed labelling of ventral side, see Fig. 84d. AZM = distal end of adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirrus, CV = contractile vacuole, MA = macronuclear nodule, MI = micronucleus, RMR1–3 = right marginal rows, 1, 2 = dorsal kineties 1 and 2. Page 483.

belonging to a kitchen garden (Eigner 1995). Type species of *Neogeneia* Eigner, 1995.

Remarks: Eigner (1995) separated *N. hortualis* from *N. costata*, inter alia, by the body length (70–90 µm in life and 68–84 µm after protargol impregnation vs. 100–130 µm in life according to Kahl 1932). However, he overlooked that *N. costata* sensu Wang & Nie (1935) is, like *N. hortualis*, only 75–100 µm long in life, that is, body size is obviously nonviable for the separation (for further problems

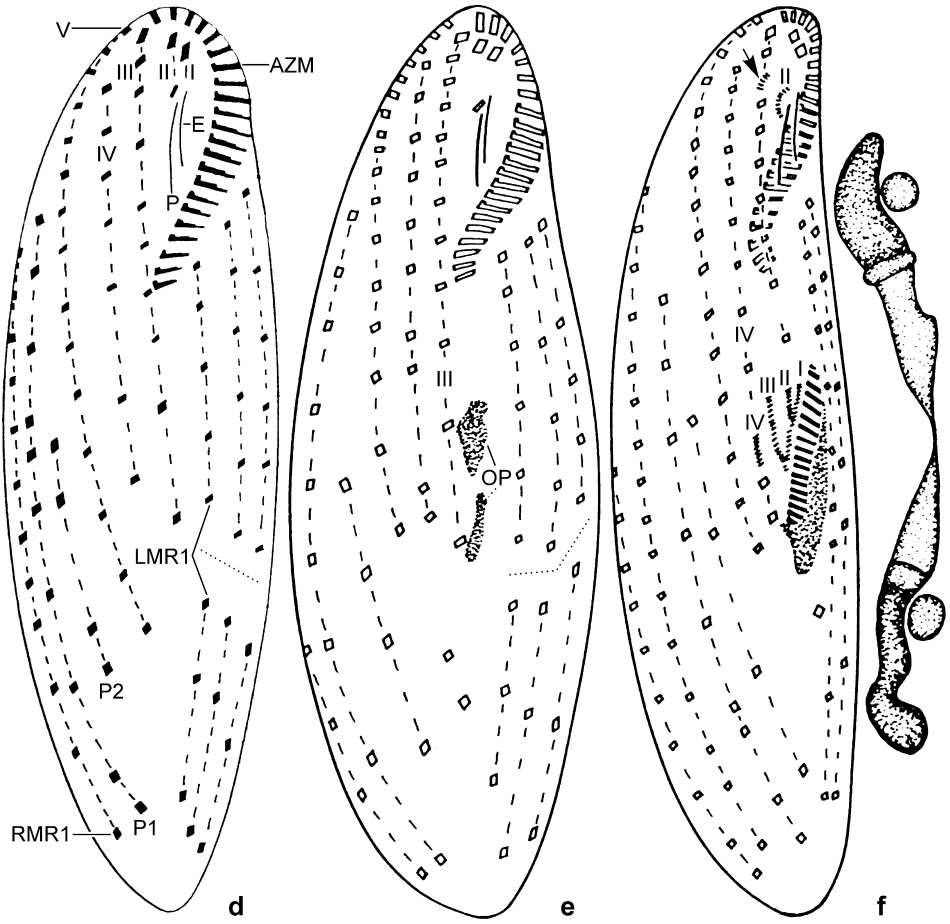

Fig. 84d–f *Neogeneia hortualis* (from Eigner 1995. Protargol impregnation). Cirri originating from the same anlage are connected by a broken line. Dotted line separates cirri of the current (ahead of line) and the parental (behind) generation. **d:** Same specimen as Fig. 84b, but with detailed labelling. **e, f:** Infraciliature of ventral side and nuclear apparatus of early dividers, e = 103 µm, f = 109 µm. Arrow in (f) denotes anlage III of proter. AZM = adoral zone of membranelles, E = endoral, LMR1 = innermost left marginal row, P = paroral, P1, P2 = parental right marginal rows (= parental and grandparental RMR1), OP = oral primordium, RMR1 = innermost right marginal row, I–V = frontoventral rows or anlagen I–V. Page 483.

with size, see footnote d in Table 27). Thus, the number of cirral rows (about 13 vs. about 7), the structure of the cell surface (smooth vs. distinctly ribbed), the shape of the macronuclear nodules (sausage-shaped vs. ellipsoidal), and the defecation vacuole in the posterior body end (lacking vs. present) are the key features for separation of *N. hortualis* and *N. costata*. The number of dorsal kineties (2 vs. 3 in *N. costata* [estimated from live observations only]) is still too uncertain. Further populations have to be studied to show whether these two species are valid or synonymous.

Morphology: Body size in life 70–90 × 25–35 µm, length:width ratio 3.0:1 on average in protargol preparations (Table 27; for problems with morphometry, see footnote d in Table 27). Body outline elliptical, inconspicuously tapering posteriorly; both ends moderately widely rounded. Body inconspicuously flattened dorsoventrally, rather stiff. Two long, almost sausage-shaped macronuclear nodules, connected by fine thread; longitudinally arranged slightly left of or in midline; anterior nodule usually shorter than posterior and curved; individual nodules with spherical chromatin bodies; each nodule usually with one spherical micronucleus 4–6 µm across (Fig. 84a). Contractile vacuole about in mid-body close to left cell margin. Cortical granules lacking. Cytoplasm with lipid inclusions 2 µm across and 6–7 µm-sized food vacuoles. Movement not described.

Adoral zone occupies about 30% of body length (Table 27), on average composed of 22 membranelles of usual fine structure (Fig. 84a, b). Buccal cavity flat and narrow. Undulating membranes slightly curved and arranged in parallel, right of middle portion of adoral zone and distinctly terminating ahead of level of buccal vertex. Membranes about of same length, but endoral commences slightly more anteriorly than paroral. Pharyngeal fibres form conspicuous sac at proximal portion of adoral zone.

Cirri about 15 µm long, generally rather widely spaced, connected by conspicuous fibres. Three enlarged frontal cirri behind distal portion of adoral zone. Buccal cirrus of same size as ventral and marginal cirri, immediately ahead of paroral. Parabuccal row (= frontoventral row III) extends slightly behind mid-body in specimen illustrated (Fig. 84b). Cirral row IV slightly shortened anteriorly, terminates about at same level as parabuccal row in specimen illustrated. Cirral row V commences about at level of frontal cirri, extends to about 70% of body length (Fig. 84b). Next two rows consisting exclusively of cirri of previous generations (inner and outer parental row; details see cell division), more or less distinctly shortened anteriorly and posteriorly; perhaps some further cirri of previous generations present forming a somewhat irregular pattern. Next cirral rows are the right marginal rows 1 (= inner row), 2 (= middle row), and 3 (= outer row; Fig. 84b). Anterior portion of right marginal row 3 composed of dorsal bristles (see next paragraph). 3–5 left marginal rows, composed of new (anterior portion) and parental cirri (posterior portion (Fig. 84b). Further details see cell division.

Two bipolar dorsal kineties, arranged mainly left of midline, that is, rather large blank area between kinety 2 and right marginal row 3. Length of dorsal bristles not described, according to Fig. 84c about 3 µm. One caudal cirrus at rear end of dorsal kinety 1, in line with rear end of outermost left marginal row and therefore not recognisable as caudal cirrus in interphasic specimens (Fig. 84c). Anterior portion of right marginal row 3 composed of about 3–4 dorsal bristles; whether this bristle row is a progenitor or vestige of a dorsomarginal kinety or nothing of the sort is not known.

Cell division (Fig. 84e–n): The morphogenesis is described in great detail by Eigner (1995). The process is relatively complicated because of the rather high number of rows and the retention of parental cirri. For comparison of the terms used in

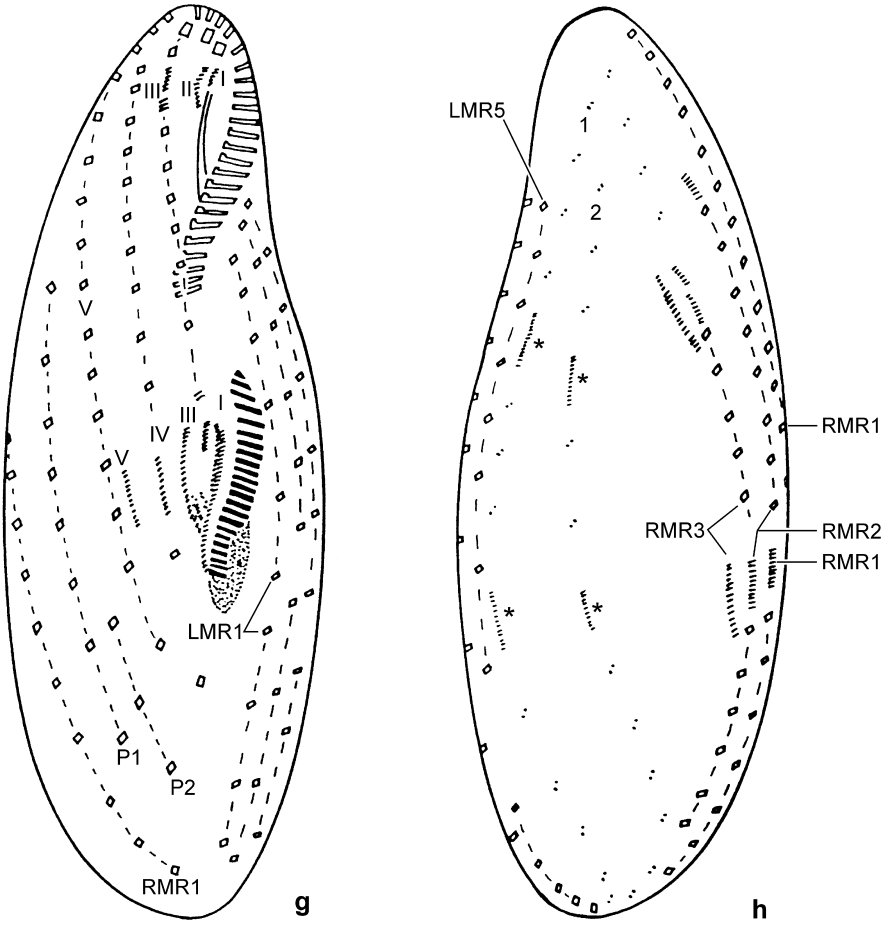

Fig. 84g, h *Neogeneia hortualis* (from Eigner 1995. Protargol impregnation). Infraciliature of ventral and dorsal side of middle divider, 102 µm. Cirri originating from same anlage connected by broken line. Asterisks mark dorsal kinety anlagen. Anlage V of the opisthe originates very likely somewhat left of the current frontoventral row V (g), that is, de novo. Note that the anlagen for the right marginal row 2 originate within the current right marginal row 3, and the anlagen for the right marginal row 1 originate within the current right marginal row 2. The anlagen for the right marginal row 3 originate (likely) de novo. LMR1, 5 = innermost and outermost left marginal row, P1, P2 = parental right marginal rows, RMR1–3 = right marginal rows or anlagen, I–V = frontoventral rows or anlagen I–V, 1, 2 = dorsal kineties. Page 483.

the present book and the original description, see Table 26. Note that some cirri have the same designation as in 18-cirri hypotrichs (e.g., Fig. 2a; Fig. 6a in Berger 1999) when they can be unambiguously homologised. The investigation of the ontogenesis of a second population is recommended to show how stable the features are.

Stomatogenesis: This part of the cell division commences with the formation of two closely spaced fields left of the rearmost two cirri of the parabuccal row (= frontoventral row III; Fig. 84e). In the next stage illustrated, the formation of new adoral

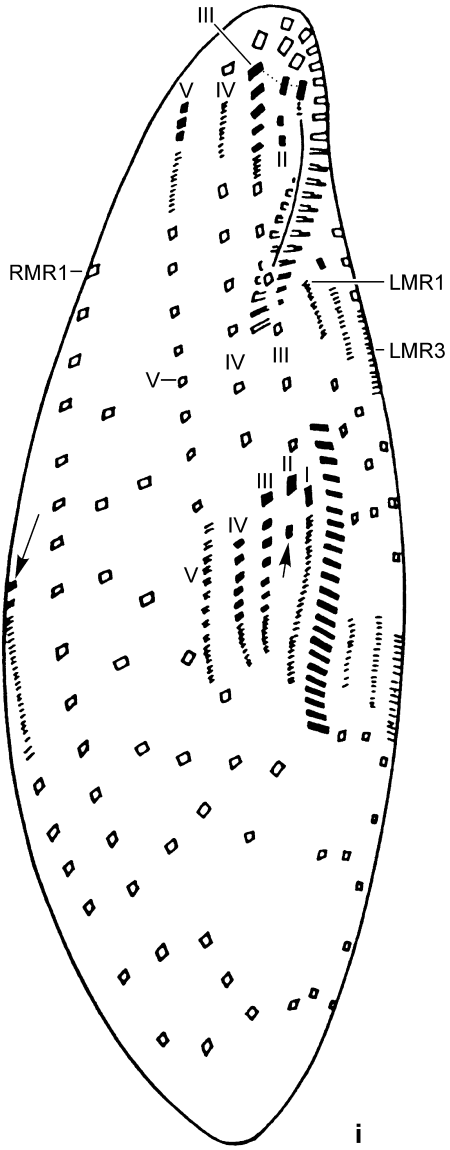

Fig. 84i *Neogeneia hortualis* (from Eigner 1995. Protargol impregnation). Infraciliature of ventral side of middle divider, 109 µm. Short arrow marks buccal cirrus of opisthe (in proter two buccal cirri are present at this stage; however, only one is retained in interphase; Table 27). Long arrow denotes the anlage of the innermost right marginal row (RMR1) of the opisthe within the current right marginal row 2. Parental structures white, new black. LMR1, 3 = anlagen of left marginal rows, RMR1 = right marginal row 1 which becomes the outer parental row (P1) when division is finished, I–V = frontoventral rows or anlagen I–V. Page 483.

membranelles is in progress (Fig. 84f). The anlagen I–III of the opisthe have separated from the oral primordium. Later, the remaining adoral membranelles are produced and the two undulating membranes (paroral and endoral) are formed from anlage I. In middle dividers, the parental undulating membranes obviously have fused or they lie on top of each other (Fig. 84i; details not mentioned in text). In late dividers, two undulating membranes are again recognisable in the proter (Fig. 84j). The parental adoral zone is obviously retained for the proter without or without distinct reorganisation (Fig. 84j, m).

Frontoventral rows I–V of opisthe: The cirral rows/anlagen I–III of the opisthe originate, as in most hypotrichs, from the oral primordium (Fig. 84f, g). Anlage I forms the undulating membranes and the left frontal cirrus (I/1); anlage II forms the middle frontal cirrus (II/3) and the buccal cirrus (II/2); and anlage III forms the right frontal cirrus (III/3) and the parabuccal row (= frontoventral row III). About at the same time, anlage IV of the opisthe originates within the frontoventral row IV right of the oral primordium (Fig. 84f). Somewhat later, anlage V is formed de novo left of the parental frontoventral row V (Fig. 84g). This was observed in four specimens (Eigner 1995). Next, anlage V of the opisthe lengthens either by disaggregation and involvement of parental cirri of the frontoventral row V or, possibly, by de novo-formed cirri (Eigner 1995; Fig. 84i). The anlagen form the new cirri, which arrange in the species specific pattern.

Frontoventral rows I–V of proter: The formation of the frontoventral row anlagen

in the proter proceeds as follows (Fig. 84f, g, i): anlage I is obviously produced from/close to the anterior end of the parental undulating membranes; this anlage forms the left frontal cirrus (I/1). Anlage II originates from the modified parental buccal cirrus; it forms the new middle frontal cirrus (II/3) and the new buccal cirrus (II/2). Anlage III is formed in the anterior portion (obviously third cirrus from anterior) of frontoventral row III (Fig. 84f, arrow); it forms the right frontal cirrus (III/3) and the parabuccal row. Anlage IV is formed from some anterior cirri of frontoventral row IV (Fig. 84i). Anlage V originates from the anterior portion of frontoventral row V (Fig. 84i). This ontogenetic activity indicates that this row is homologous to row/anlage V of the 18-cirri hypotrichs or species forming six frontal-ventral-transverse cirri anlagen (I–VI) because the anteriormost cirri of row VI (frontoterminal cirri) are never involved in primordia formation. That is, *Neogeneia hortualis* very likely has lost anlage VI. Later, the cirral streaks lengthen and form the final cirral pattern. Obviously, few parental cirri are retained at the end of the rows (Fig. 84j, m).

Right marginal rows: Eigner (1995) did not distinguish between frontoventral rows and right marginal rows (Table 26). I suppose that the three rightmost cirral rows are marginal rows because of the position and the clear separation from the five centrally located (frontoventral) rows. The formation of the right marginal row anlagen begins in middle dividers (Fig. 84h). The anlagen for the (new) right marginal row 1 (= inner right marginal row) originate within the parental marginal row 2 (Fig. 84h, i); the anlage for the proter is formed at the anterior end, that for the opisthe about at the level of the frontoventral row anlagen. The anlagen for the (new) right marginal rows 2 originate within the parental right marginal row 3 (Fig. 84h). By contrast, the anlagen for the (new) outermost right marginal row (= new right marginal row 3) are formed left[1] of the anlagen for the new right marginal rows 2 (Fig. 84h, i). According to Eigner (1995, p. 351) the anlagen for row 3 are formed "neokinetal 1".[2] The specimen shown in Fig. 84m, n demonstrates that no cirri of the right marginal rows 2 and 3 are retained in postdividers. The parental right marginal row 1 (= innermost right marginal row) is not involved in primordia formation (Fig. 84g–i). It is retained and separated into two parts, the anterior one becomes the outer parental row (P1 in Fig. 84d) of the proter, the posterior one becomes the outer parental row of the opisthe. After the next division, the outer parental rows become the inner parental rows. Older cirri are resorbed so that the number of rows remains constant. This process and the fact that the anlagen of rows 1 and 2 are not formed within the parental row, but in the neighbouring row or more or less de novo (right marginal row 3) causes a rather complex ontogenetic pattern, a so-called neokinetal wave (Eigner 1995). Eigner (1995, p. 361) writes that this wave shifts the outermost

[1] Eigner (1995) wrote "*right* of the anlagen 7" which is obviously incorrect. Since the anlagen are formed on the dorsal side, *left* is correct.

[2] Eigner (1995, p. 342) defined neokinetal 1 as follows: One anlage develops within a cirral row and an additional anlage develops parallel to it. Later, Eigner (1997, p. 555) modified the definition of neokinetal 1. According to Eigner (1997), neokinetal 1 is a (the?) major apomorphy of the Parakahliellidae, a group comprising many species with dorsal kinety fragmentation, *Parakahliella macrostoma* (p. 407), *Amphisiellides illuvialis* (see Berger 2008, p. 569), and the present species.

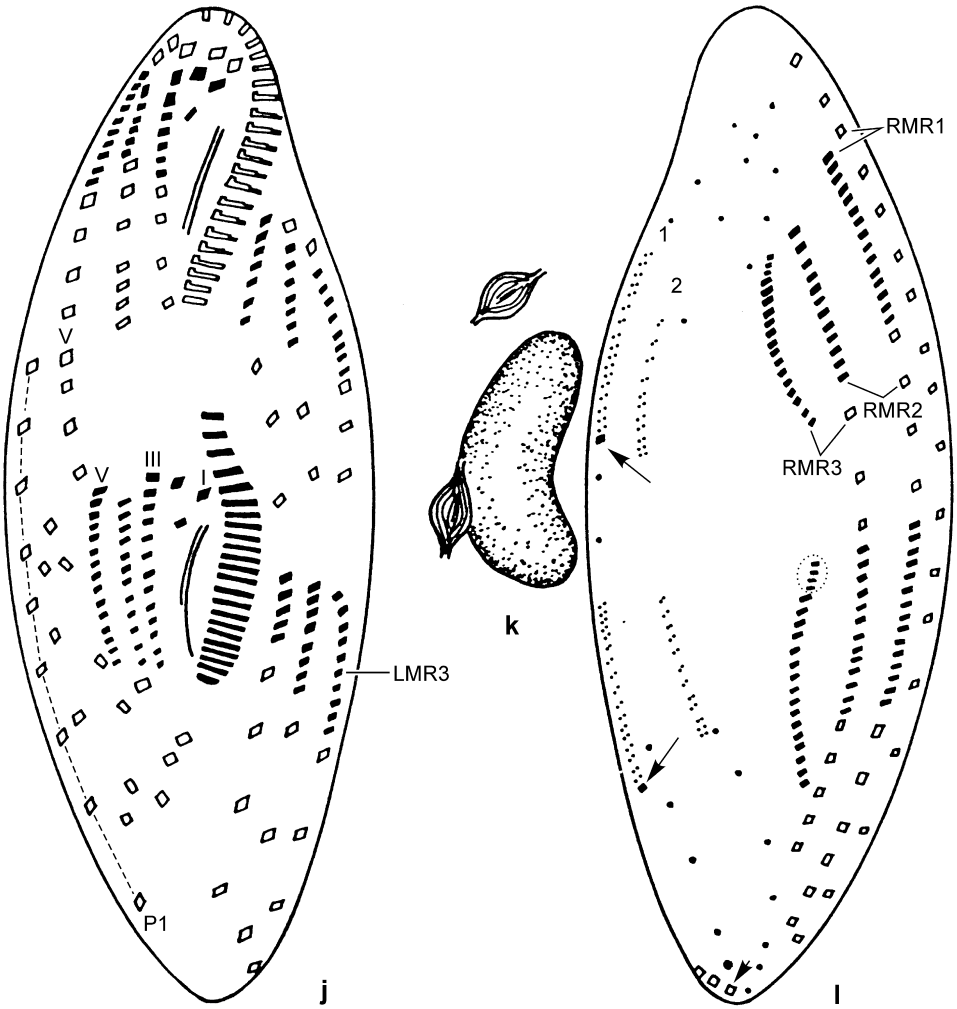

Fig. 84j–l *Neogeneia hortualis* (from Eigner 1995. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of late divider, 103 µm. Parental structures white, new black. Long arrows mark new caudal cirri, short arrow denotes parental caudal cirrus, which is indistinguishable from the outermost left marginal row in interphasic specimens. The anterior portion of the outermost right marginal row (RMR3) is composed of dorsal bristles (dotted circle). LMR3 = anlage of left marginal row 3 of opisthe, P1 = old right marginal rows, RMR1–3 = right marginal rows and their anlagen, I, III, V = frontoventral row anlagen I, III, and V of opisthe, 1, 2 = dorsal kineties with anlagen. Page 483.

right marginal row (RMR3) to the left in each of the following four generations. I suppose however, that this interpretation is not quite correct because obviously no cirri of rows 2 and 3 are retained in the next generation (Fig. 84m).

Left marginal rows: In middle dividers each two anlagen (one for the proter and one for the opisthe) occur within the left marginal rows (Fig. 84i, j). Eigner (1995,

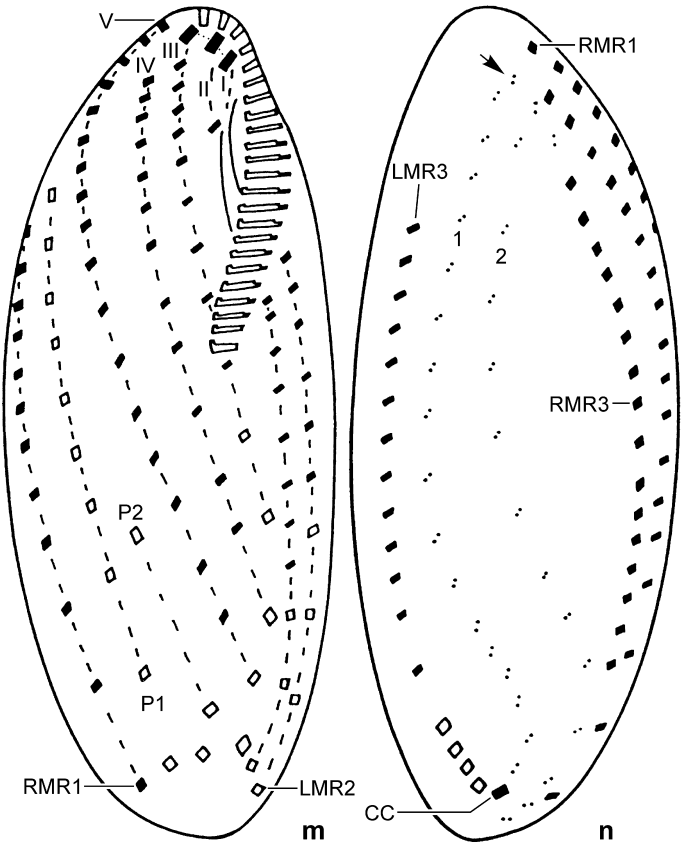

Fig. 84m, n *Neogeneia hortualis* (from Eigner 1995. Protargol impregnation). Infraciliature of ventral and dorsal side of postdivider, 77 µm (proter according to parental adoral zone). Arrow in (n) marks dorsal bristles ahead of right marginal row 3 (dorsomarginal kinety? see text). Broken lines connect cirri originating from same anlage. Frontal cirri connected by dotted line. Parental structures white, new black. CC = caudal cirrus, LMR2, 3 = left marginal rows (note that each left marginal row is composed of new and parental cirri), P1, 2 = old right marginal rows (explanation see text), RMR1, 3 = right marginal rows, I–V = frontoventral rows I–V, 1, 2 = dorsal kineties. Page 483.

p. 352) wrote that the streaks develop between the cirri, which would mean that the formation is de novo. I suppose that each anlage is initiated, as is usual, at least by one parental cirrus. However, behind each anlage several parental cirri are retained, which later form the posterior portion of the left marginal rows (Fig. 84d, i, j, m). Eigner (1995) termed this process "neokinetal 2". According to Eigner (1995, p. 352) most of the parental left marginal cirri shown in Fig. 84d, g (cirri behind dotted line in Fig. 84d) are resorbed, whereas the cirri of the current generation (left marginal cirri ahead of dotted line in Fig. 84d) are retained. This anterior half of the left marginal rows is split by the anlagen for the opisthe and later forms the posterior portion of the left marginal rows. However, I am not quite sure that this interpretation is correct because the left marginal row anlagen for the opisthe are formed about at the level where the current and the parental portions meet (Fig. 84d, g, i). Perhaps in the opisthe the rear portion is composed of parental and grandparental cirri.

Dorsal kineties: *Neogeneia hortualis* has two bipolar dorsal kineties and some dorsal bristles ahead of the outermost right marginal row (= right marginal row 3;

Fig. 84c). Kineties 1 and 2 are formed by the common way, that is, within each kinety two anlagen (one for the proter and one for the opisthe) are produced (Fig. 84h, l, n). At the end of kinety 1, one caudal cirrus is formed, which is arranged immediately behind the outermost left marginal row (Fig. 84l, n). Thus, it cannot be recognised as caudal cirrus in non-dividers (Fig. 84c). Some basal body pairs bearing dorsal bristles are formed at the anterior end of the new right marginal row 3 (Fig. 84h, l, n). This position is retained in interphasic specimens (Fig. 84c). Whether these bristles are a progenitor or a vestige of a dorsomarginal kinety is not known. The same pattern is also described for few other species.

Nuclear apparatus: The division of the nuclear apparatus proceeds in the ordinary manner, that is, replication bands occur, the macronuclear nodules fuse to a single mass, and later divide into the species-specific number (Fig. 84f, k).

Occurrence and ecology: Terrestrial. So far, *Neogeneia hortualis* is only recorded from the type locality, which is in the village "Schrötten bei Deutsch-Goritz" (46°47'N 15°49'E; 320 m altitude), Styria, Austria. Eigner (1995) discovered it there in a compost heap of a kitchen garden in March 1992. Eigner (1995) wrote that the "wet sample" was treated as described for *Deviata abbrevescens*, that is, he put the sample into a Petri dish and added local spring water[1] (pH 7.4, 20 °C, 1.9 mg l^{-1} $KMnO_4$), squeezed wheat grains, and baker's yeast. Feeds on bacteria (Eigner 1995). Biomass of 10^6 specimens about 38 mg (Foissner 1998, p. 206).

Neogeneia costata (Kahl, 1932) Eigner, 1995
(Fig. 85a–f)

1932 ***Kahlia costata* spec. n.** – Kahl, Tierwelt Dtl., 25: 546, Fig. 86_{26}, 91 (Fig. 85a, b; original description; no type material available).

1935 ***Kahlia costata* Kahl 1932** – Wang & Nie, Sinensia, 6: 483, Fig. 60, 61 (Fig. 85c, d; description of Chinese population).

1960 ***Kahliella costata* (Kahl, 1932)** – Corliss, J. Protozool., 7: 275 (combination with *Kahliella*).

1968 ***Kahliella costata* (Kahl, 1932) Corliss, 1960** – Chorik, Free-living ciliates, p. 122, Fig. 109 (Fig. 85e; guide to ciliates in Moldovan water bodies).

1982 ***Kahlia costata* Kahl, 1932** – Hemberger, Dissertation, p. 28 (revision of hypotrichs).

1987 ***Kahliella costata* (Kahl) Corliss, 1960** – Lokot, Ökologie der Wimpertiere, p. 68, Fig. 22 (Fig. 85f; illustrated record).

1992 ***Kahliella costata* (Kahl, 1930–5) Corliss, 1960** – Carey, Marine interstitial ciliates, p. 174, Fig. 684 (redrawing of Fig. 85a; guide).

1995 ***Neogeneia costata* (Kahl, 1932) nov. comb.** – Eigner, Europ. J. Protistol., 31: 361 (combination with *Neogeneia*).

2001 ***Neogeneia costata* (Kahl, 1932) Eigner, 1995** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 40 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

[1] Eigner (1995) made not comment whether or not the spring water was sterilised before it was added. When it was not sterilised, it cannot be excluded that *N. hortualis* was in the spring water and not in the soil sample. Further, a compost heap is usually a mixture of local material (e.g., soil and plants from the garden) and external material which has its origin often far away, as, for example, used, imported flower soil. Consequently, it is not certain that the compost heap in Eigner's garden is indeed the type locality (ICZN 1999, Article 76.1.1).

Nomenclature: The species-group name *costat·us*, *-a*, *-um* (Latin adjective [m; f; n]; corrugated, ribbed) obviously refers to the body surface ("ectoplasm"), which has distinct ribs (Kahl 1932). In the spelling "*Kahliella costata* Kahl 1934" of Chardez (1988, p. 9), the author has to be placed in parenthesis; further, the year is incorrect.

Remarks: Kahl (1932) classified this species in *Kahlia* (now *Kahliella*, p.347) because of the lack of transverse cirri and the presence of some enlarged frontal cirri as well as some (five) ventral cirral rows, which resemble marginal rows. Later it has been recorded three times from other limnetic habitats; however, a detailed redescription is still lacking.

According to Hemberger (1982), *Kahlia costata* is a junior synonym of *Kahliella acrobates* (p. 354) because the cirral pattern is identical and the morphological particularities (ribs? defecation vacuole?) do not allow a separation; perhaps the shorter adoral zone can serve as distinctive feature. *Uroleptopsis multiseta* Dragesco, 1970, classified as synonym of *K. acrobates* in the present book, is similar in this respect (Hemberger 1982; Fig. 63a, b). However, this species has more (unenlarged) cirri on the frontal field.

Eigner (1995), who did not discuss previous descriptions of *K. costata*, transferred it to *Neogeneia* because it resembles *N. hortualis* in body shape, the habitat (compost heap vs. rotting macrophytes in pond) and likely also because of the cirral pattern. I preliminary accept the classification in *Neogeneia*, although it is as sure or uncertain as that in *Kahliella*.

Neogeneia costata differs from the type species in body length (100–130 µm according to Kahl 1932 [however, only 75–100 µm according to Wang & Nie 1935] vs. 70–90 µm [see also footnote d in Table 27]), number of cirral rows (7 vs. 11–13), and the shape of the two macronuclear nodules (ellipsoidal vs. sausage-shaped connected by fine thread). In addition, Kahl (1932) described distinct ribs between the cirral rows, a feature not mentioned in the original description of *N. hortualis*. According to Kahl (1932), the present species has invariably(?) a distinct defecation vacuole in posterior body portion, a feature verified by Wang & Nie (1935) and Lokot (1987). However, all differences – including the dorsal kineties (3 vs. 2) – have to be confirmed by a detailed redescription of *N. costata*.

The description of a Chinese population by Wang & Nie (1935) agrees well with the original description so that the identification is basically beyond reasonable doubt. The major differences are (i) in the position of the ribs, namely between the cirral rows, that is, on the ventral side according to Kahl (1932), but on the dorsal side according to Wang & Nie (1935); and (ii) in the consistency of the body (rather rigid vs. elastic and more or less changeable). Further studies are needed to decide which of the two observations is correct. The descriptions by Chorik (1968) and Lokot (1987) are brief and in Russian and therefore only marginally considered in the next chapter.

Morphology: Body length of type population 100–130 µm, length:width ratio of specimens illustrated 2.9–4.0:1 (Fig. 85a, b; Kahl 1932); Chinese population some-

what smaller, that is, 75–100 × 25–30 µm (Wang & Nie 1935). Body shape slender oval to almost cylindrical, that is, dorsoventrally only inconspicuously flattened; both ends usually rounded. Body rather rigid (Kahl 1932) or elastic and more or less changeable, that is, oval when contracted and elongate-elliptical when fully extended (Wang & Nie 1935). Ectoplasm (Kahl (1932) or endoplasm (Wang & Nie 1935) colourless to yellowish, shining. According to Kahl (1932), between each two cirral rows a distinct rib. According to Wang & Nie (1935, p. 484), dorsal side with four or five longitudinal ribs or ridges; however, on p. 485 they write that ribs, which are about of body length, may be clearly seen between two rows of ventral cirri and the number is difficult to determine because the cell is flexible and metabolic. Ribs composed of ectoplasm only, give the cell a sharp brilliant lustre especially when moving (Wang & Nie 1935). Two macronuclear nodules about in cell centre; individual nodules ellipsoidal to ovoid (Fig. 85a–c); in some specimens each nodule seems to be composed of two equal halves (Fig. 85d); each nodule associated with a globular, rather large micronucleus. Contractile vacuole somewhat displaced inwards about at level of anterior macronuclear nodule. Invariably a defecation vacuole in rear body end (Kahl 1932; Fig. 85a, b); non-contractile, contains several or many minute crystal-like bodies suspended in a kind of liquid, whether or not this vacuole has excretory function could not be determined by Wang & Nie (1935; Fig. 85c, d). No cortical granules described in type and Chinese population. Endoplasm granular, transparent, and colourless or slightly yellowish; food vacuoles or particles usually crowded in posterior body portion (Wang & Nie 1935). Movement not described.

Adoral zone occupies about 20–25% of body length (Fig. 85a–d). Buccal field rather small and narrow; prominent buccal lip[1] covers proximal portion of adoral zone (Fig. 85a, b). Paroral distinct, at base of buccal lip (Fig. 85a); paroral cilia of Chinese population very fine and short (Fig. 85d). Cytopharynx short.

Cirral pattern only known from live observations, that is, details should not be overinterpreted. Five or six enlarged cirri on frontal field, namely, three frontal cirri, one buccal cirrus, and one (Fig. 85a, b) or two (Fig. 85c, d) parabuccal cirri. According to Kahl (1932), each one (marginal) row per side dorsolaterally and about five ventral rows. According to Wang & Nie (1935) ventral cirri numerous and arranged in five longitudinal rows. Transverse cirri lacking. Marginal and ventral cirri bristle-like (Kahl 1932), that is, long and stiff (Wang & Nie 1935). Cirral rows equidistantly and cirri within rows loosely arranged.

According to Kahl (1932) probably three dorsal kineties present; bristles "long and thin".[2] "Dorsal cirri exceedingly fine and short, very numerous arranged in five longitudinal rows" in Chinese population; I suppose that these five rows correspond the two marginal rows and the three kineties described by Kahl (1932). According to

[1] Kahl (1932) emphasised that the right margin of the frontal field is raised from the ventral side very distinctly. The term frontal field is not clearly defined; probably it is the buccal field/cavity in Kahl (1932). Thus, he obviously meant the buccal lip which is very conspicuous according to the illustrations (Fig. 85a, b).

[2] Normal ("short") dorsal bristles are about 2–4 µm long. Thus, "long" bristles are five or more micrometres long.

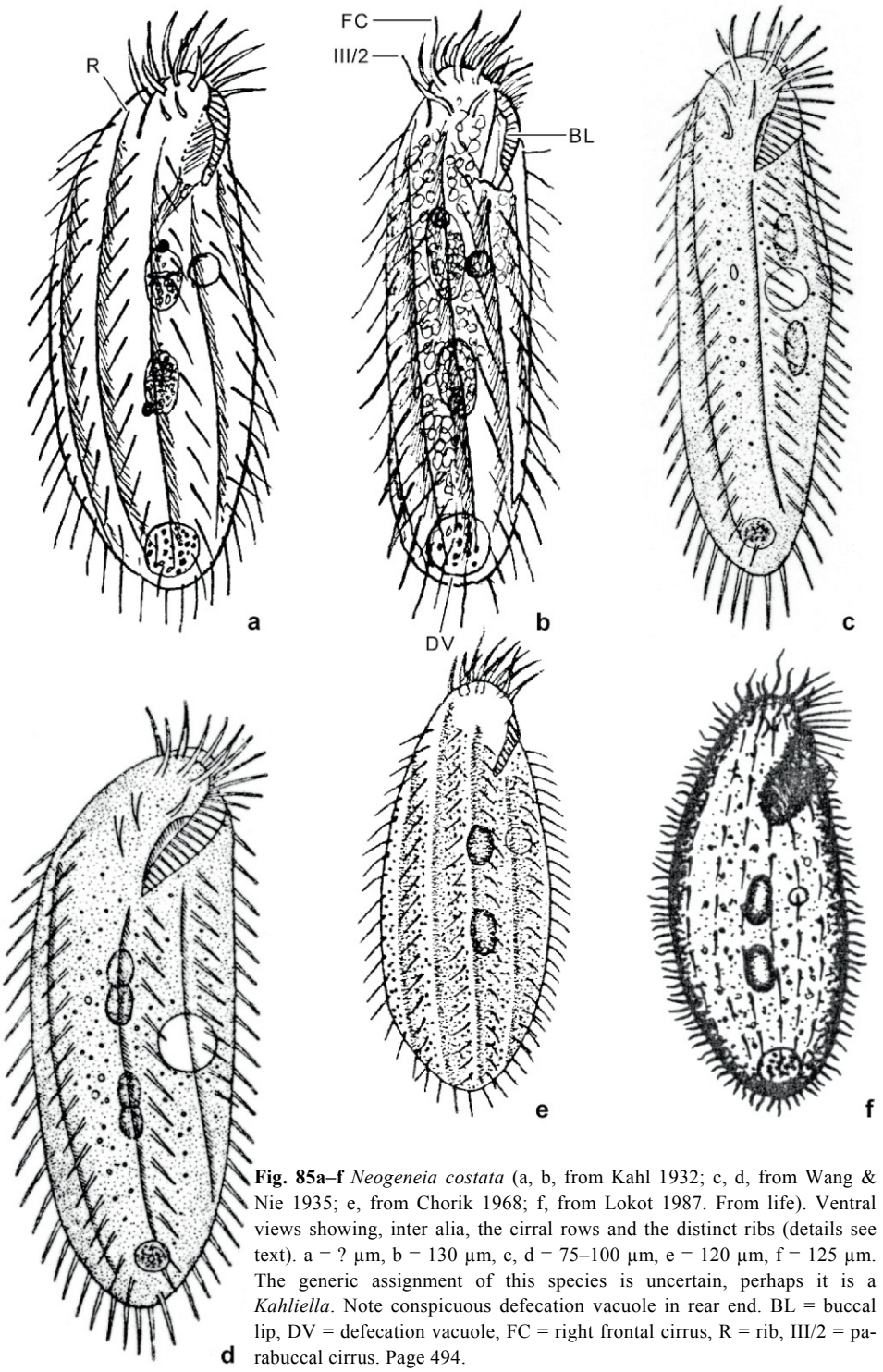

Fig. 85a–f *Neogeneia costata* (a, b, from Kahl 1932; c, d, from Wang & Nie 1935; e, from Chorik 1968; f, from Lokot 1987. From life). Ventral views showing, inter alia, the cirral rows and the distinct ribs (details see text). a = ? µm, b = 130 µm, c, d = 75–100 µm, e = 120 µm, f = 125 µm. The generic assignment of this species is uncertain, perhaps it is a *Kahliella*. Note conspicuous defecation vacuole in rear end. BL = buccal lip, DV = defecation vacuole, FC = right frontal cirrus, R = rib, III/2 = parabuccal cirrus. Page 494.

Wang & Nie (1935), the cirri/bristles on the dorsal side are arranged on or very close to the ridges.

Population/specimen described by Chorik (1968) about 120 × 40 µm. Six cirral rows. No defecation vacuole in posterior body portion (Fig. 85e).

Occurrence and ecology: Limnetic; so far *Neogeneia costata* is only recorded from the Holarctic. Type locality is the pond in the botanical garden of the city of Hamburg, Germany, where Kahl (1932) discovered it in rotting macrophytes (*Nymphaea*, *Glyceria*) rather regularly during winter.

Records substantiated by morphological data: Moldovan water bodies (Chorik 1968); limnetic habitats in Lake Baikal area (Lokot 1987); once in high abundance among submerged vegetation and decaying organic substances in a pool near the Mo T'zu Hospital in Nanking (China) during Mid-October 1934 (Wang & Nie 1935).

Records not substantiated by morphological data: rare on parts of *Sphagnum* from a mesotrophic lake (Heiliges Meer) near the city of Münster, Germany (Mücke 1979, p. 273); Kuchurgansk cooling plant, Moldavia (Chorik & Vikol 1973, p. 68). Chardez (1988, p. 9) mentioned *Kahliella costata* in a paper about criminology. Marine records are certainly misidentifications: Lagoon of Venice, Italy (Coppellotti & Matarazzo 2000, p. 426); psammophilous in the Kandalakshskij Bay, White Sea (Burkovsky 1970, p. 11; 1970a, p. 56). Likely because for that records, Carey (1992) listed *N. costata* in his guide to marine interstitial ciliates.

Neogeneia costata feeds on bacteria, single-celled algae, and very minute ciliates (Wang & Nie 1935).

Engelmanniella Foissner, 1982

1982 ***Engelmanniella* nov. gen.**[1] – Foissner, Arch. Protistenk., 126: 66 (original description). Type species (by original designation): *Uroleptus mobilis* Engelmann, 1862.
1985 ***Engelmanniella*** – Small & Lynn, Phylum Ciliophora, p. 456 (guide to ciliate genera).
1987 ***Engelmanniella* Foissner, 1982** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (classification of hypotrichs).
1990 ***Engelmanniella*** [2] – Wirnsberger-Aescht, Foissner & Foissner, Arch. Protistenk., 138: 47 (improved diagnosis).
1994 ***Engelmanniella* Foissner, 1982** – Tuffrau & Fleury, Traite de Zoologie, 2: 137 (classification of hypotrichs).
1995 ***Engelmanniella* Foissner, 1982** [3] – Eigner, Europ. J. Protistol., 31: 363 (improved diagnosis; redefinition of the Kahliellidae).

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[1] Foissner (1982) provided the following diagnosis: Sehr schlanke, wurmförmige, wenig abgeflachte Oxytrichidae (?) mit mindestens 2 rechten und 2 linken Marginalreihen und wenig differenzierten Frontalcirren. Makronucleus zwei- bis mehrteilig. Interphaseindividuen ohne morphologisch differenzierte Ventral- und Transversalcirren.

[2] Wirnsberger-Aescht et al. (1990) provided the following improved diagnosis: Infraciliature consisting of frontal, parabuccal, buccal, and marginal cirri. Somatic cirral rows comprise 3 generations of cirri. A dorsal kinety develops de novo in the opisthe.

[3] Eigner (1995) provided the following improved diagnosis: More than one long cirral row on right and left side of body. At least one of them is typically parental (old) on each side. A short dorsal kinety develops de novo during morphogenesis. Neokinetal wave to the left on both sides of adoral zone of membranelles.

1999 ***Engelmanniella* Foissner, 1982** – Berger, Monographiae biol., 78: 893 (brief note on exclusion from Oxytrichidae).
1999 ***Engelmanniella* Foissner, 1982** – Shi, Acta Zootax. sinica, 24: 251 (revision of hypotrichs).
1999 ***Engelmanniella* Foissner, 1982** – Shi, Song & Shi, Progress in protozoology, p. 98 (revision of hypotrichs).
2001 ***Engelmanniella* Foissner 1982** – Aescht, Denisia, 1: 66 (catalogue of generic names of ciliates).
2001 ***Engelmanniella* Foissner, 1982** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 20 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Engelmanniella* Foissner, 1982** [1] – Lynn & Small, Phylum Ciliophora, p. 457 (guide to ciliate genera).
2007 ***Engelmanniella* Foissner, 1982** – Jankowski, Phylum Ciliophora, p. 461 (revision of ciliate genera).
2008 ***Engelmanniella* Foissner, 1982** – Lynn, Ciliated protozoa, p. 357 (revision of ciliate families).

Nomenclature: Foissner (1982) obviously dedicated this genus to Th. Wilhelm Engelmann, the great German protozoologist (e.g., Engelmann 1862), who discovered the type species. It is a composite of the surname Engelmann, the thematic vowel *·i-*, and the diminutive suffix *-ella*. Because of this ending, *Engelmanniella* is feminine (ICZN 1999, Article 30.1.3; Aescht 2001, p. 282). Incorrect subsequent spellings: *Engelmaniella mobilis* (Engelmann) (Tirjaková 1988, p. 499; 2005, p. 21; Matis et al. 1996, p. 10); *Engelmaniella* sp. (Steinbrück & Kiy 2000; Andelová & Tirjaková 2005, p. 35); *Englemanellia halsyi* (Roberts & Causton 1988, p. 300).

Characterisation (A = supposed apomorphy): Kahliellidae(?). Body very slender, worm-like. Pellicle multilamellated (A?). Adoral zone of membranelles short, indistinctly bipartite. Paroral composed of only few cilia (A?). Three slightly enlarged frontal cirri, one buccal cirrus, short parabuccal row, and long frontoventral row present. Frontoterminal cirri, postoral ventral cirri, pretransverse ventral cirri, and transverse cirri lacking. One left and one right marginal row plus widely spaced parental and grandparental marginal cirri left of normal marginal rows. Frontoventral cirri anlagen I–III originate independently in proter and opisthe, frontoventral rows originate by two anlagen within parental row. Less than three bipolar dorsal kineties; a short dorsal kinety near right cell margin develops from parental row in proter, but de novo in the opisthe (A). Caudal cirri, dorsal kinety fragmentation, and dorsomarginal row lacking. Limnetic and terrestrial.

Remarks: *Engelmanniella* is a monotypic genus based on *Uroleptus mobilis*, a species already described by Engelmann (1862). However, just Foissner (1982) in his important paper on soil hypotrichs provided a detailed description of the ventral and dorsal infraciliature. Actually, the cirral pattern is relatively simple, but in spite of that it looks rather complicated due to some rows of widely spaced cirri in the lateral areas. Wirnsberger-Aescht et al. (1989) demonstrated that these widely spaced cirri are remnants of the marginal rows of the parental and grandparental generation.

Foissner (1982) assigned *Engelmanniella* to the Oxytrichidae, however, with doubt and without foundation. Somewhat later, Small & Lynn (1985) classified it in their newly established family Cladotrichidae (Table 4; for diagnosis see footnote 2

[1] Lynn & Small (2002) provided the following characterisation: Midventral surface bare; at least one ventral cirral file extending adjacent to left marginal cirral file, which may be on dorsal surface.

on p. 51), because *E. mobilis* basically agrees with *Cladotricha koltzowii* as redescribed by Borror & Evans (1979, Fig. 43m), except for the widely spaced cirri, which are lacking in *Cladotricha*. Likely because of the lack of transverse cirri, the meridional (untwisted) arrangement of the cirral rows, and the widely spaced parental cirri, which are also present in *Kahliella*, Tuffrau (1987) transferred *Engelmanniella* to the kahliellids, a classification followed by Foissner & Foissner (1988, p. 82), Tuffrau & Fleury (1994), Eigner (1995, p. 363), Shi (1999), Shi et al. (1999), Lynn & Small (2002), Jankowski (2007), Lynn (2008), and the present review (see below). Wirnsberger-Aescht et al. (1989, 1990) supposed that *Engelmanniella* descends from a kahliellid lineage, and because of many uncertainties they refrained from the establishment of a new family with *Engelmanniella* as name-bearing type. Eigner (1997) assigned it to the Orthoamphisiellidae; however, because of distinct differences in cell division (e.g., long cirral rows formed from single anlage in *Orthoamphisiella* vs. from two in *Engelmanniella*; anlagen II and III of opisthe originate from proter anlagen vs. from independent anlagen), the classification was only provisionally. The kahliellids were submerged in the oxytrichids by Eigner (1997).

Indeed, it is rather difficult to estimate the phylogenetic position of *Engelmanniella*, although "almost everything" is known about this species. The preservation of cirri of previous generations suggests a classification in the kahliellids (see above). However, in *Kahliella simplex* the parental cirri of frontoventral row VI are displaced rightwards, that is, towards the right marginal row whereas in *Engelmanniella* the parental right marginal rows are displaced leftwards towards the frontoventral row, that is, on the right side of the cell the situation is rather different in *Kahliella* and *Engelmanniella*. By contrast, on the left side the neokinetal wave moves in the same direction in both genera. However, there are some further differences, which are briefly discussed. *Engelmanniella* lacks a dorsomarginal kinety, whereas this part of the dorsal infraciliature is present in *K. simplex* (Fig. 65g, 70h, k), a species very similar or perhaps even synonymous with the type species *K. acrobates*. In addition, the oral primordium of *E. mobilis* originates de novo (Fig. 89b), while in close contact or from the parental frontoventral rows in *Kahliella* (Fig. 70a, b). So far, no phylogenetic tree containing both genera is available. Kim et al. (2010) included a *Kahliella* sp. in a tree mainly dealing with oligotrichs, but also containing 11 hypotrichs. They found that *Kahliella* is closely related to *Halteria grandinella* and *Oxytricha granulifera*, type of *Oxytricha*. By contrast, *Engelmanniella* was considered in several molecular analyses, which, however, revealed rather various positions, indicating that the true origin was not yet found (see below).

According to Shi et al. (1999) and Shi (1999), *Deviata* Eigner, 1995 is a junior synonym of *Engelmanniella*. However, this is certainly incorrect for several reasons, for example, *Deviata* does not retain parental cirri and there are rather distinct differences in cell division (e.g., oral primordium originates from parental row vs. de novo).

Engelmanniella mobilis has a multilamellate pellicle (Wirnsberger-Aescht et al. 1989; Fig. 90a–c). The innermost layer is likely the ordinary cell membrane, where-

as the other layers are stacks of perilemma, the sole (main?) apomorphy of the Perilemmaphora Berger, 2008, that is, the group comprising the oligotrichs + hypotrichs. An increased number of membrane layers (up to 16 on dorsal side) is also reported in *Epiclintes auricularis* (Carey & Tatchell 1983; for review, see Berger 2006a, p. 1119). But according to molecular analyses by Hu et al. (2009b), *Epiclintes* and *Engelmanniella* are not closely related. However, since only very few hypotrichs are analysed ultrastructurally a thorough discussion of this feature (synapomorphy? synplesiomorphy? convergence?) is unrewarding at the present state of knowledge. The previous discussion shows that the phylogenetic position of *E. mobilis* is difficult to estimate because neither morphological and ontogenetic data nor molecular features provide a reliable and stable position with the Hypotricha tree. Consequently, I use a pragmatic solution and follow Tuffrau (1987) and many other workers and preliminary classify *E. mobilis* in the kahliellids, mainly because of the preservation of parental cirri.

As already mentioned above, *Engelmanniella mobilis* has basically a rather simple cirral pattern, inter alia, characterised by a very long cirral row extending from right of the parabuccal cirri to near the rear cell end. Especially the extension to near the cell end makes it difficult to find the correct designation for this row, namely, inner right marginal row or frontoventral row. Two features more or less clearly indicate that it is not an ordinary right marginal row, namely, (i) anlagen within this row originate distinctly later than in the "true" marginal rows (Fig. 89f–i); and (ii) no parental cirri of this row are retained in postdividers, as this is the case with the "true" marginal rows of *Engelmanniella*. The formation of this row proceeds basically identical as in the ordinary marginal rows, that is, two independent anlagen occur, one for the proter and one for the opisthe. The same terminological problem is present in some other genera, for example *Cladotricha*, where the long rows right of the parabuccal row are designated as frontoventral rows (e.g., Fig. 48g). Thus, the long cirral row immediately right of the parabuccal row is named frontoventral row in *E. mobilis*. In previous papers on *Engelmanniella*, this row was termed as follows: second cirral row right of the median ("2. Cirrenreihe rechts der Medianen"; Foissner 1982); right marginal row 1 (Wirnsberger-Aescht et al. 1989); long rightmost ventral row four (Eigner 1997). Further details on the disorienting terminology, see footnote c in Table 28. For synonymy of *E. mobilis*, *Uroleptus mobilis americanus*, and *U. halseyi* as well as comparison with similar species, see remarks at *Engelmanniella mobilis*.

Species included in *Engelmanniella* (basionym is given): (1) *Uroleptus mobilis* Engelmann, 1862.

Species misplaced in *Engelmanniella*: The following species does not belong to *Engelmanniella*.

Engelmanniella kahli (Grolière, 1975) Foissner, 1982. Remarks: Now *Perisincirra kahli* (Grolière, 1975) Jankowski, 1978, type of *Perisincirra* (p. 471).

Key to *Engelmanniella mobilis* and similar forms

Although *Engelmanniella* comprises only the type species, I provide a short key including two populations illustrated and briefly described, but not validly published by Kahl (1932), because they have a similar body shape and nuclear apparatus. Further slender forms, see *Neogeneia* (p. 481), *Deviata* (p. 555), *Circinella* (p. 309), *Perisincirra* (p. 463), and *Hemisincirra* (Berger 2008, p. 387).

1 Body very slender with many(?) macronuclear nodules (Fig. 77d in Berger 2008, p. 395). . . . . *Uroleptus* (?) spec. sensu Kahl (1932; p. 545)
- Body not so extremely slender; about 5–16 (rarely up to 26) macronuclear nodules (Fig. 86a–d, 87a, b, 88a, 95a). **2**

2 Cortical granules ordinary, in longitudinal rows (Fig. 87a–f, 90d). . . . . *Engelmanniella mobilis* (p. 502)
- Cortical granules conspicuous, along marginal rows (Fig. 95a). . . . . *Uroleptus* spec. sensu Kahl (1932; p. 544)

Engelmanniella mobilis (Engelmann, 1862) Foissner, 1982
(Fig. 86a–t, 87a–f, 88a–d, 89a–q, 90a–g, 91a–m, 92a–h, 93a–f, 94a–c, Tables 28–30)

1862 ***Uroleptus mobilis* n. sp.**[1] – Engelmann, Z. wiss. Zool., 11: 386[2], Tafel XXXI, Fig. 11, 12 (Fig. 86a, b; original description; no type material available).

1882 ***Uroleptus mobilis*, Eng.** – Kent, Manual infusoria, p. 781, Plate XLIII, Fig. 9, 10 (Fig. 86a, b; revision).

1901 ***Uroleptus mobilis* Englm.** – Roux, Mém. Inst. natn. génev., 19: 99, Planche VI, fig. 2 (Fig. 86c; description of Swiss population).

1919 ***Uroleptus mobilis*, Engelm.** – Calkins, J. exp. Zool., 27: 293, Fig. 1–95 (Fig. 86d, h, i; description of New York Variety, including history of nuclear apparatus during division and conjugation).

1919 ***Uroleptus mobilis* Engelm.** – Calkins, J. exp. Zool., 29: 121, Fig. 1–4, Table 1–6 (Fig. 86d–g; renewal of vitality through conjugation of New York Variety).

1926 ***Uroleptus mobilis*** – Calkins, Biology of the Protozoa, p. 37, 466, Fig. 16, 194–196 (Fig. 94a–c; formation of doublets).

1929 ***Uroleptus halseyi*, n. sp.** – Calkins, Biol. Bull., 57: 59, Fig. 2–6, Tables on p. 64, 66 (Fig. 86j–l; original description of synonym; no formal diagnosis provided and very likely no type material available).

1929 ***Uroleptus mobilis* Engel. New York variety** – Calkins, Biol. Bull., 57: 61, Fig. 1 (Fig. 86m; comparison with *U. mobilis* and *U. halseyi*; see nomenclature and remarks).

1930 ***Uroleptus halseyi* Calkins** – Calkins, Arch. Protistenk., 69: 151, Fig. 1, Plate 11, Fig. 1–8, Plate 12, Fig. 9–21 (Fig. 86n, o; details on nuclear apparatus).

1932 ***Uroleptus mobilis* Engelmann, 1861** – Kahl, Tierwelt Dtl., 25: 548, Fig. 101$_2$ (Fig. 86p; revision; incorrect year).

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[1] Engelmann (1862) provided the following diagnosis: Körper formbeständig, biegsam; drehrund, etwa zwölfmal so lang als breit, nach hinten allmählich stumpf zugespitzt. Randwimpern überall gleich lang. Sechs längliche Kerne.

[2] I have an original reprint of the paper and in this reprint the original description begins on page 40.

1932 ***Uroleptus mobilis* var. *americanus* var. provis. Calkins, 1929** – Kahl, Tierwelt Dtl., 25: 548, Fig. 92_2 (Fig. 86r; formal original description for New York variety described by Calkins 1929, see nomenclature).

1932 ***Uroleptus halseyi* Calkins, 1929** – Kahl, Tierwelt Dtl., 25: 548, Fig. 92_1 (Fig. 86q; revision).

1954 ***Uroleptus halseyi*** – Mote, Proc. Iowa Acad. Sci., 61: 588, Plate VII, Fig. 24 (Fig. 86t; illustrated record from Iowa).

1954 ***Uroleptus mobilis* var. *americanus*** – Mote, Proc. Iowa Acad. Sci., 61: 588, Plate VII, Fig. 25 (Fig. 86s; illustrated record from Iowa).

1972 ***Uroleptus mobilis* Engelmann** – Nikoljuk & Geltzer, Procvennye prostejsie SSSR, p. 130, Plate XII, Fig. 234 (redrawing[?] of Fig. 86p; illustrated record from USSR soil).

1972 ***Uroleptus mobilis* Engelmann, 1862** – Borror, J. Protozool., 19: 19 (revision of hypotrichs; see remarks).

1972 ***Uroleptus halseyi* Calkins, 1929** – Borror, J. Protozool., 19: 19 (revision of hypotrichs; see remarks).

1972 ***Uroleptus americanus* Calkins, 1919** – Borror, J. Protozool., 19: 19 (raise from variety to species rank; revision of hypotrichs; incorrect year, see nomenclature and remarks).

1982 ***Engelmanniella mobilis* (Engelmann, 1862)** – Foissner, Arch. Protistenk., 126: 66, Abb. 14a–f, 57–59, Tabelle 14 (Fig. 87a–f; detailed redescription and combination with *Engelmanniella*; two slides [accession numbers 1981/96, 1982/55] have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], see neotypification).

1982 ***Engelmanniella halseyi* (Calkins, 1929) nov. comb.** – Foissner, Arch. Protistenk., 126: 66 (combination with *Engelmanniella*).

1985 ***Engelmanniella mobilis*** – Small & Lynn, Phylum Ciliophora, p. 456, Fig. 23A, B (Fig. 87c, e; guide to ciliate genera).

1987 ***Engelmanniella mobilis*** – Foissner, Progr. Protistol., 2: 92, Fig. 32, 33 (Fig. 88a, b; scanning electron micrographs).

1989 ***Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982** – Wirnsberger-Aescht, Foissner & Foissner, Europ. J. Protistol., 24: 354, Fig. 1–49 (Fig. 88a–d, 89a–q, 90a–g; morphogenesis and ultrastructure of Austrian population).

1990 ***Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982** – Wirnsberger-Aescht, Foissner & Foissner, Arch. Protistenk., 138: 29, Fig. 1–27, Tables 1–3 (Fig. 91a–m, 92a–h; analysis of variability and ultrastructure of resting cyst; synonymisation of *U. halseyi* and *U. mobilis americanus* with *E. mobilis*).

1992 ***Engelmanniella americanus* (Calkins, 1929)** – Detcheva, Catalogi Faunae Bulgaricae, p. 97 (faunal catalogue).

1994 ***Engelmanniella mobilis*** – Foissner, Kataloge des O.Ö. Landesmuseums Linz, 71: 170, Abb. 5 (Fig. 88a; review about soil protozoa).

1995 ***Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982** – Eigner, Europ. J. Protistol., 31: 355, Fig. 39, 40, 48 (Fig. 86a, b, 89a; schematised representation of cell division).

1995 ***Engelmanniella mobilis*** – Foissner, Ciliaten des Bodens, p. 176, Abb. 8 (Fig. 87a; brief review on soil ciliates).

1997 ***Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982** – Eigner, J. Euk. Microbiol., 44: 558, Fig. 10 (redrawing of Fig. 89b, c; schematic representation of cell division).

2001 ***Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 98 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2002 ***Engelmanniella mobilis*** – Lynn & Small, Phylum Ciliophora, p. 457, Fig. 52A, B (Fig. 87c, e; guide to ciliate genera).

2003 ***Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982** – Dragesco, Trav. Mus. Hist. nat. Gr. Antipa, 45: 24, Fig. 43–46, Tableau 11 (Fig. 93a–f; description of population from Rwanda).

2009 ***Engelmanniella mobilis*** – Foissner, Protozoological Monographs, 4: 213, Fig. 8 (Fig. 87a; brief review on soil ciliates).

Table 28 Morphometric data on *Engelmanniella mobilis* (Gn, natural population from Grafenwörth, Foissner 1982; Bn, natural population from Baumgarten; Jc, cultured population from Japan; Jn, natural population from Japan; Tc, cultured population from Turkey; Tn, natural population from Turkey; populations Bn to Tn from Wirnsberger-Aescht et al. 1990; Rw, from Dragesco 2003)

Characteristics [a]	Pop [f]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	Bn	121.2	120.0	10.3	2.1	8.5	96.0	143.0	25
	Gn	136.5	135.0	24.1	6.7	17.7	94.0	196.0	13
	Jn	146.0	145.0	9.3	2.4	6.3	130.0	161.0	15
	Jc	187.3	190.0	16.6	4.3	8.8	153.0	218.0	15
	Rw	156.0	152.0	20.2	3.2	13.0	100.0	210.0	41
	Tc	221.7	229.0	32.4	8.4	14.6	177.0	283.0	15
	Tn	134.7	128.0	23.3	6.0	17.3	107.0	193.0	15
Body, width	Bn	17.1	17.0	2.1	0.4	12.2	13.0	21.0	25
	Gn	14.7	15.0	1.6	0.4	10.8	13.0	17.0	13
	Jc	17.9	17.0	2.7	0.7	14.8	14.0	22.0	15
	Jn	23.8	24.0	2.4	0.6	10.0	20.0	29.0	15
	Rw	24.5	23.0	4.1	0.6	16.0	19.0	35.0	41
	Tc	21.0	20.0	4.2	1.1	20.0	16.0	31.0	15
	Tn	15.3	16.0	2.1	0.5	13.6	12.0	19.0	15
Macronuclear nodules, number	Bn	7.2	8.0	1.2	0.2	16.6	5.0	8.0	25
	Gn	8.1	8.0	0.3	0.1	3.3	8.0	9.0	13
	Jc	12.8	13.0	2.2	0.6	17.5	8.0	16.0	15
	Jn	7.1	7.0	0.8	0.2	11.3	5.0	8.0	15
	Rw	9.0	9.0	2.1	0.3	23.0	6.0	14.0	45
	Tc	10.9	10.0	2.3	0.6	20.9	8.0	15.0	15
	Tn	8.4	8.0	0.7	0.2	8.8	8.0	10.0	15
Macronuclear nodule, length [e]	Bn	10.4	10.0	2.1	0.4	20.5	7.0	15.0	25
	Gn	8.3	8.0	1.7	0.5	20.0	6.0	12.0	13
	Jc	10.5	10.0	3.0	0.8	28.9	7.0	20.0	15
	Jn	10.5	10.0	3.0	0.8	28.9	7.0	20.0	15
	Rw	7.7	8.0	1.6	0.2	21.0	4.8	12.0	41
	Tc	10.5	9.0	4.3	1.1	40.5	5.0	20.0	15
	Tn	8.4	8.0	1.8	0.5	21.9	6.0	13.0	15
Macronuclear nodule, width [e]	Bn	3.8	4.0	0.7	0.1	18.3	3.0	6.0	25
	Gn	3.1	3.0	0.9	0.2	27.3	1.5	4.2	13
	Jc	2.9	3.0	0.7	0.2	22.2	2.0	4.0	15
	Jn	5.0	5.0	0.4	0.1	8.1	4.0	6.0	15
	Tc	3.6	3.0	0.6	0.2	17.6	3.0	5.0	15
	Tn	3.2	3.0	0.7	0.2	21.3	2.0	4.0	15
Micronuclei, number	Bn	3.1	3.0	0.8	0.2	26.3	2.0	4.0	25
	Gn	2.4	2.0	0.5	0.1	20.4	2.0	3.0	13
	Jc	5.3	5.0	1.2	0.3	23.1	3.0	8.0	15
	Jn	3.4	4.0	1.2	0.3	34.7	2.0	6.0	15
	Rw	2.6	3.0	1.0	0.2	41.0	1.0	6.0	21
	TC	3.5	4.0	0.8	0.2	23.5	2.0	5.0	15
	Tn	1.6	2.0	0.6	0.2	39.4	1.0	3.0	15
Micronucleus, length	Bn	2.0	2.0	0.4	0.1	20.2	2.0	3.0	25
	Gn	3.6	3.5	0.7	0.2	19.8	2.6	5.3	13
	Jc	2.4	3.0	0.4	0.1	17.3	2.0	3.0	15
	Jn	2.0	2.0	0.1	0.0	6.4	2.0	3.0	15
	Tc	4.4	4.0	1.2	0.3	26.1	3.0	7.0	15
	Tn	4.7	5.0	1.1	0.3	23.8	3.0	7.0	15

Table 28 Continued

Characteristics [a]	Pop [f]	Mean	M	SD	SE	CV	Min	Max	n
Micronucleus, width	Bn	1.9	2.0	0.4	0.1	18.1	2.0	3.0	25
	Gn	2.4	2.0	0.6	0.1	23.6	1.8	4.0	13
	Jc	2.0	2.0	0.1	0.0	6.4	2.0	3.0	15
	Jn	1.8	2.0	0.2	0.1	13.1	2.0	2.0	15
	Tc	2.8	3.0	0.4	0.1	13.4	2.0	3.0	15
	Tn	2.2	2.0	0.5	0.1	22.4	2.0	3.0	15
Adoral membranelles, number	Bn	20.6	20.0	0.9	0.2	4.2	19.0	22.0	25
	Gn	21.5	22.0	2.3	0.6	19.6	16.0	25.0	13
	Jc	23.4	23.0	1.4	0.4	6.0	21.0	26.0	15
	Jn	24.8	25.0	1.0	0.3	4.1	23.0	27.0	15
	Tc	25.3	25.0	1.5	0.4	6.1	23.0	28.0	15
	Tn	19.8	19.0	1.2	0.3	5.8	18.0	22.0	15
	Rw	22.0	23.0	5.0	0.8	23.0	19.0	27.0	58
Adoral zone of membranelle, length	Bn	22.4	22.0	1.2	0.2	5.3	21.0	25.0	25
	Gn	22.1	23.0	3.5	1.0	15.9	14.0	26.0	13
	Jc	33.3	32.0	2.2	0.6	6.6	31.0	37.0	15
	Jn	35.2	35.0	2.2	0.6	6.3	30.0	39.0	15
	Rw	36.5	36.0	5.1	0.8	14.0	26.0	48.0	41
	Tc	35.6	35.0	3.0	0.8	8.3	31.0	42.0	15
	Tn	25.2	25.0	2.1	0.6	8.5	22.0	29.0	15
Frontal cirri, number	Gn	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
	Rw[d]	6.5	7.0	0.9	0.1	13.0	5.0	8.0	34
Buccal cirri, number	Gn	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Cirral rows, total number	Rw[d]	6.6	7.0	0.5	0.1	7.5	6.0	7.0	21
Cirral rows right of midline, number	Gn[b]	4.0	4.0	0.0	0.0	0.0	4.0	4.0	13
Cirral rows left of midline, number	Gn	2.1	2.0	0.4	0.1	16.7	2.0	3.0	13
Parabuccal row, number of cirri [c]	Bn	3.7	4.0	0.6	0.1	16.4	3.0	5.0	25
	Gn	3.5	4.0	0.8	0.2	24.3	2.0	5.0	13
	Jc	4.2	4.0	–	–	–	4.0	5.0	15
	Jn	5.4	5.0	0.8	0.2	15.4	4.0	7.0	15
	Tc	4.9	5.0	0.7	0.2	15.2	4.0	6.0	15
	Tn	4.0	4.0	0.9	0.2	21.3	3.0	6.0	15
Frontoventral row, number of cirri [c]	Bn	31.1	31.0	2.6	0.5	8.3	26.0	38.0	25
	Gn	33.8	36.0	5.1	1.4	15.1	24.0	43.0	13
	Jc	40.3	41.0	3.8	1.0	9.3	34.0	48.0	15
	Jn	38.5	38.0	2.7	0.7	7.1	35.0	44.0	15
	Rw	38.0	37.0	2.7	0.6	7.0	34.0	44.0	21
	Tc	46.0	47.0	5.3	1.4	11.4	36.0	55.0	15
	Tn	30.8	31.0	2.5	0.6	8.1	26.0	35.0	15
Grandparental right marginal row, number of cirri [c]	Bn	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25
	Gn	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13
	Jc	1.0	1.0	0.0	0.0	0.0	1.0	1.0	3
	Jn	5.1	5.0	1.6	0.4	31.4	2.0	8.0	14
	Tc	1.6	4.0	3.9	1.8	245.0	2.0	15.0	5
	Tn	1.7	1.0	2.0	0.7	119.4	1.0	7.0	9
Parental right marginal cirral row, number of cirri [c]	Bn	11.6	10.0	3.6	0.7	30.8	5.0	20.0	25
	Gn	14.4	15.0	5.7	1.6	39.6	5.0	25.0	15
	Jc	20.7	21.0	4.3	1.1	20.7	12.0	28.0	15
	Jn	14.7	15.0	3.6	0.9	24.3	7.0	24.0	15
	Tc	17.9	16.0	6.7	1.7	37.5	9.0	30.0	15

Table 28 Continued

Characteristics [a]	Pop [f]	Mean	M	SD	SE	CV	Min	Max	n
Parental right marginal cirral row number of cirri [c]	Tn	9.5	10.0	2.6	0.7	27.2	5.0	13.0	15
Right marginal row, number of cirri [c]	Bn	37.4	38.0	3.8	0.0	10.2	26.0	46.0	25
	Gn	34.6	35.0	5.1	1.4	14.7	26.0	48.0	13
	Jc	44.9	46.0	4.5	1.2	10.1	35.0	53.0	15
	Jn	42.5	43.0	2.0	0.5	4.8	39.0	46.0	15
	Tc	47.3	49.0	6.0	1.6	12.7	36.0	58.0	15
	Tn	34.5	34.0	2.6	0.7	7.7	30.0	40.0	15
Left marginal row, number of cirri [c]	Bn	29.0	29.0	4.1	0.8	14.2	21.0	37.0	25
	Gn	27.0	27.0	4.6	1.3	17.0	17.0	35.0	13
	Jc	34.6	35.0	4.5	1.2	12.9	26.0	44.0	15
	Jn	34.9	35.0	3.6	0.9	10.2	30.0	43.0	15
	Tc	38.9	41.0	6.9	1.8	17.6	26.0	52.0	15
	Tn	26.2	25.0	3.7	1.0	14.2	22.0	37.0	15
Parental left marginal row, number of cirri [c]	Bn	6.5	6.0	3.4	0.7	52.0	3.0	19.0	25
	Gn	10.8	8.0	5.3	1.5	48.8	6.0	24.0	13
	Jc	16.7	17.0	3.5	0.9	21.1	11.0	21.0	15
	Jn	13.5	12.0	5.8	1.5	43.0	7.0	23.0	15
	Tc	16.7	14.0	6.9	1.8	41.2	9.0	28.0	15
	Tn	8.6	7.0	3.3	0.8	38.0	5.0	14.0	15
Grandparental left marginal row, number of cirri [c]	Bn	6.1	6.0	1.9	0.4	31.1	3.0	11.0	25
	Gn	5.5	6.0	–	–	–	5.0	6.0	2
	Jc	9.0	9.0	2.5	0.6	27.9	5.0	13.0	15
	Jn	6.6	6.0	2.3	0.6	35.2	3.0	11.0	15
	Tc	5.6	5.0	4.5	1.2	80.9	1.0	14.0	14
	Tn	3.8	4.0	2.9	0.8	76.6	1.0	11.0	13
Cirri on caudal area, number	Gn	3.8	4.0	0.8	0.2	20.0	3.0	5.0	12
	Rw	3.4	3.0	0.6	0.1	17.0	3.0	5.0	21
Dorsal kineties, number	Gn	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known), SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] Parabuccal row (= row behind frontal cirrus) included.

[c] In other papers (Foissner 1982 / Wirnsberger-Aescht et al. 1989, 1990 / Eigner 1997) the cirral rows have the following designation: Parabuccal row in present book = 1st right row / parabuccal row / ventral cirral row 3. Frontoventral row in present book = 2nd right row / 1st right marginal row / long rightmost ventral cirral row four. Parental right marginal row in present book = 3rd right row / 2nd right marginal row / no designation. Right marginal row in present book = 4th right row / 3rd right marginal row / right marginal row (= cirral row 5). Left marginal row in present book = 1st left row / left marginal row 1 / left marginal row (L1). Parental left marginal row in present book = 2nd left cirral row 1 / left marginal row 2 / no designation. Grandparental left marginal row in present book = 3rd left row / left marginal row 3 / no designation.

[d] The number of frontal cirri comprises the frontal cirri, the buccal cirrus, and the parabuccal cirri. In the number of cirral rows the parabuccal row is not included, but the two dorsal kineties are included.

[e] In the populations studied by Wirnsberger-Aescht et al. (1990), the median nodule was measured.

[f] The natural populations studied by Wirnsberger-Aescht et al. (1990) are from air-dried soil samples remoisted with distilled water for about 6 d. The “cultured” Turkish and Japanese populations were cultured for three months (details see occurrence and ecology).

Nomenclature: *Uroleptus mobilis* is the type species of the monotypic genus *Engelmanniella* Foissner, 1982. No derivation of the names *mobilis* and *americanus* is given in the original descriptions. The species-group name *mobil·is*, *-is*, *-e* (Latin adjective [m; f; n]; mobile) obviously refers to the fact that the species lively moves and creeps like a snake among plant debris (Engelmann 1862). Kahl (1932) established the provisional variety "*Uroleptus mobilis* var. *americanus* var. provis." for the "New York variety of *U. mobilis*" described by Calkins (1919a, 1929). Calkins, 1929". The name *american·us*, *-a*, *-um* (Latin adjective [m; f; n]; American, living in America) refers to the continent or country where the variety was discovered (New York, USA). Kahl (1932) unambiguously introduced only a formal name for the variety described by Calkins (1929), that is, the description is from Calkins. Thus, "Calkins in Kahl, 1932" is the author (ICZN 1999, Recommendation 51E); Wirnsberger-Aescht et al. (1990, p. 29, 47) were of different opinion and assigned the variety to Kahl (1932). Due to the establishment of the variety *U. mobilis americanus*, the autonym (nominotypical variety) *U. mobilis mobilis* Engelmann, 1862 was created simultaneously (Winston 1999, p. 330). Although Foissner (1982) did not formally transfer *U. mobilis americanus* to *Engelmanniella*, he is automatically also the combining author for all subspecific taxa, that is, for the two varieties: *Engelmanniella mobilis mobilis* (Engelmann, 1862) Foissner, 1982 and *Engelmanniella mobilis americana* (Calkins in Kahl, 1932) Foissner, 1982 (see also Wirnsberger-Aescht et al. 1990, p. 29, 47). Borror (1972) and Detcheva (1992) considered the New York variety as distinct species (see list of synonyms); if this decision is accepted, then the correct name in *Engelmanniella* is *E. americana* (Calkins in Kahl, 1932) Foissner, 1982 (note that Borror 1972 incorrectly assigned the species to Calkins 1919 who, for the first time, mentioned the term New York variety; see also ICZN 1999, Article 45.6.4). Calkins (1929, p. 59) dedicated the species *U. halseyi* to his friend M. R. Halsey, who collected the sample.

Incorrect subsequent spellings: *Engelmanniella americanus* (Calkins, 1929) (Detcheva 1992, p. 97); *Englemanellia halsyi* (Roberts & Causton 1988, p. 300); *Uroloeptus mobilis* (Dragesco 2003, p. 24); *Uroleptus nobilis* (Gellért & Tamás 1958, p. 234); *Uroleptus halsey* (Szabo 1995, p. 19); *Uroleptus holseyi* (Szabo 1993). Neiswestnowa-Shadina (1935, p. 573) and Biczók (1955, p. 31) incorrectly mentioned Ehrenberg as author of *U. mobilis*, whereas Cairns & Yongue (1973, p. 32) erroneously mentioned Calkins as author of this species.

Neotypification: According to Aescht (2003, p. 391; 2008, p. 166), W. Foissner deposited two slides of the population studied by Foissner (1982) in the Upper Austrian Museum in Linz. Obviously, the slides have been labelled as neotypes, one also as "genotypus", which should likely indicate that *E. mobilis* is the type species of *Engelmanniella*. Foissner (1982) neither mentioned that slides have been deposited in a museum nor did he make a note about the designation of a neotype. Consequently, the qualifying conditions claimed by the relevant code (ICZN 1964, Article 75c) have not been published and therefore the neotypification obviously intended by

Table 29 Comparison of the three *Engelmanniella* taxa according to Calkins (1929)

Characteristics	Taxon		
	Uroleptus mobilis[a]	New York variety	*Uroleptus halseyi*
Body, length	300 µm	158 µm	163 µm
Body, diameter	25 µm	15.6 µm	18.7 µm
Macronuclear nodules, number	6	8–12	8–26
Macronuclear nodules, size	?	3.8 × 8.3 µm	3.2 × 8.4 µm
Micronuclei, number	?	2–6	1–2
Micronuclei, size	?	2.0–2.5 µm	2.8 × 9.3 µm
Contractile vacuole	anterior third	centre, dorsal	centre, dorsal
Tail (posterior body end)	inconspicuous	blunt, curved	pointed, curved

[a] From Engelmann (1862).

Foissner is invalid, respectively, was never made. However, a fixation of a neotype of *E. mobilis* is highly recommended for several reasons: (i) the original description by Engelmann (1862) does not agree very well with the authoritative redescriptions (e.g., Foissner 1982, Wirnsberger-Aescht et al. 1989, Dragesco 2003) in some important features (e.g., cortical granulation, exact cirral pattern); (ii) the dorsal infraciliature, a key feature for hypotrich taxonomy, of Engelmann's population is not known; (iii) a very similar species (*Uroleptus halseyi* Calkins, 1929) was described and later synonymised with *E. mobilis* by Wirnsberger et al. (1990); and (iv) no type material of Engelmann's population exists. Thus, the population studied in detail by Foissner (1982) is designated as neotype following Article 75.3 of the ICZN (1999):

(i) The taxonomic status of *E. mobilis* and *E. halseyi* is unclear because they obviously differ only in some difficult features (Table 29). At present they are considered as synonyms (Wirnsberger et al. 1990, present book). However, it cannot be excluded that populations from different continents have evolved to distinct subspecies or species during such a long time of separation. The fixation of a European population as neotype of *E. mobilis* is the first step to unravel the situation.

(ii) At the moment *E. mobilis* and *E. halseyi* are classified as synonyms, because the differences listed in Table 29 are considered, at the present state of knowledge, as insufficient for species separation. Consequently, *Engelmanniella* is monotypic. For separation from similar taxa, see remarks.

(iii) The neotype population is described in detail by Foissner (1982) and below.

(iv) It is generally known that no type material (permanent slide) is available from species originally described by Engelmann (1862). Thus, the present species was not objectively defined via a type specimen so far. Calkins (1919a, p. 298) made mainly iron-haematoxylin stains of the New York variety (Fig. 86d, m). Further, he made cross-sections showing, inter alia, some cirral rows (Fig. 86i). I found no hint in the paper that Calkins has deposited the slides in a museum, indicating that they are still somewhere in the Columbia University were Calkins worked or, more

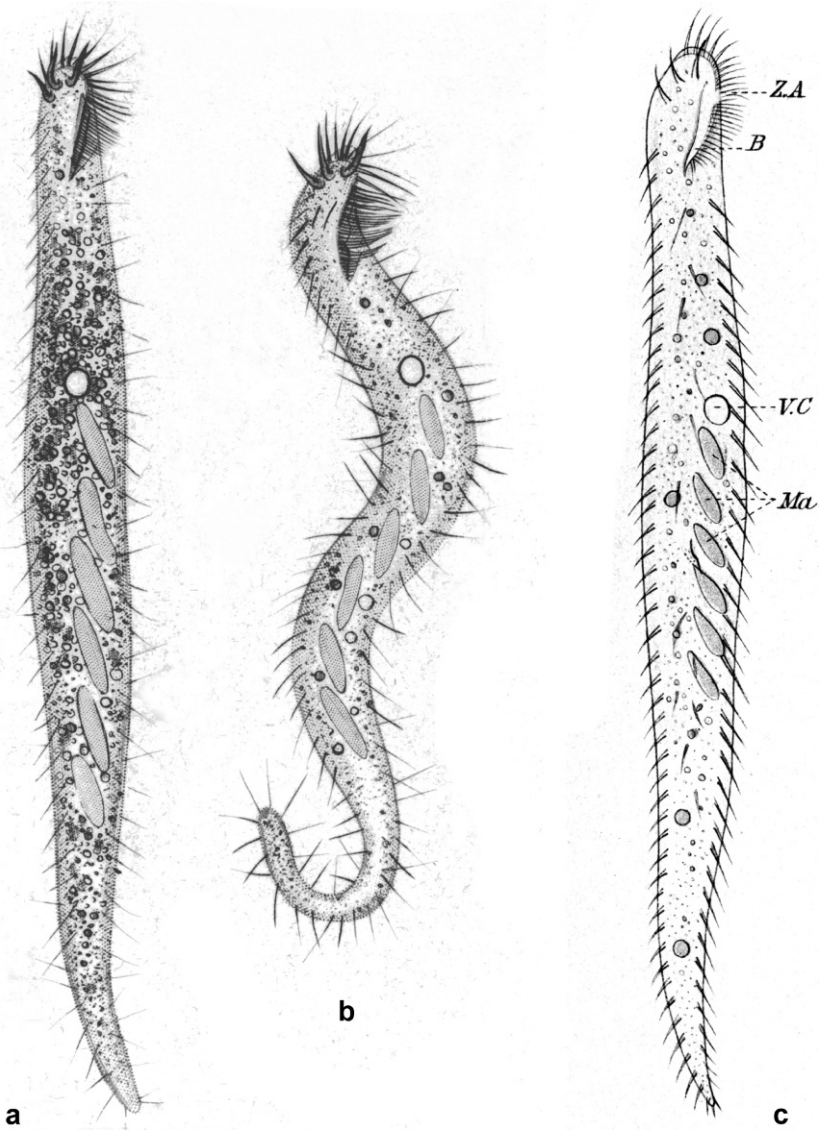
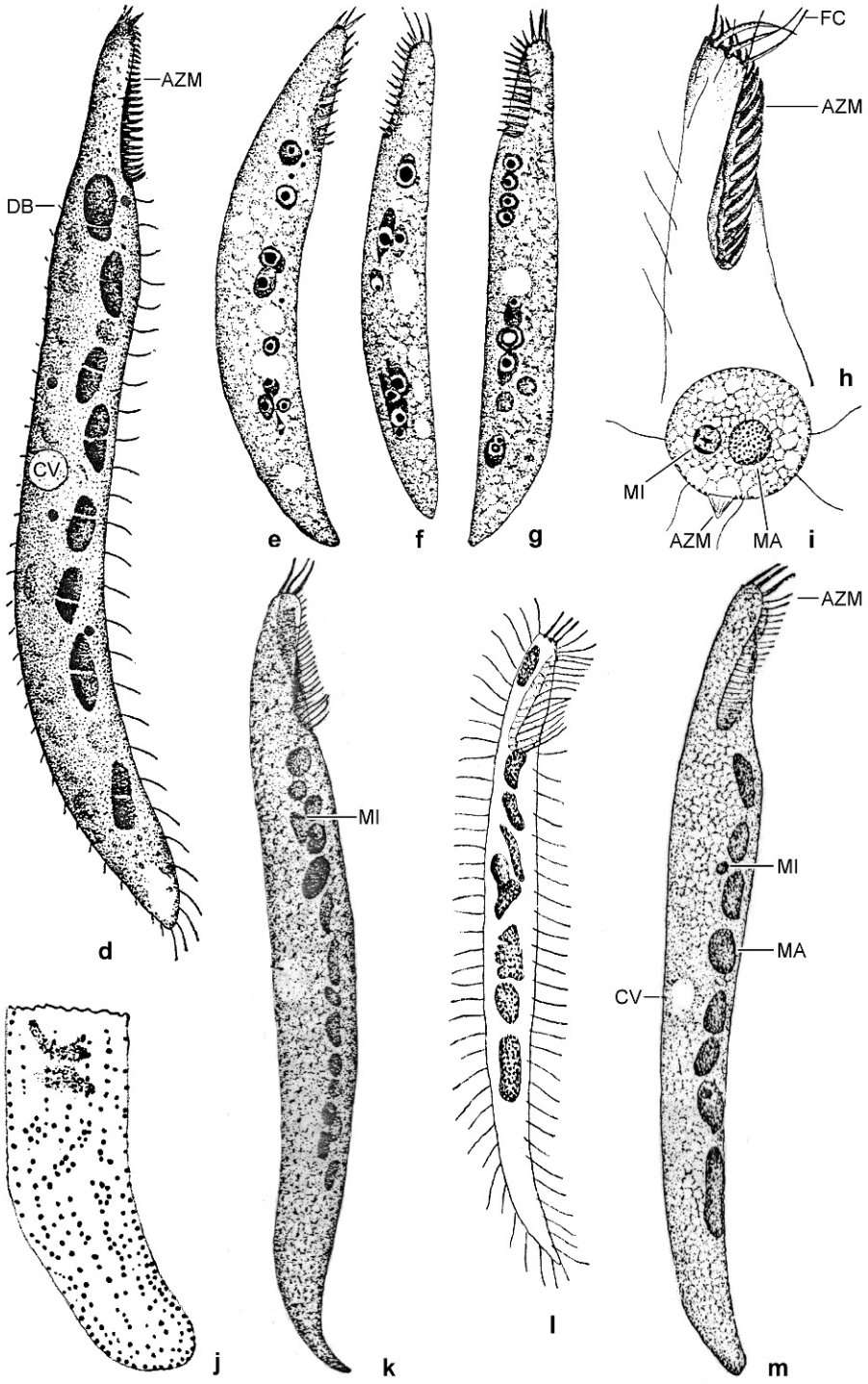


Fig. 86a–c *Engelmanniella mobilis* (a, b, from Engelmann 1862; c, from Roux 1901. From life). **a, b:** Extended and curved specimen, length on average 300 µm. **c:** Extended specimen, 350–400 µm. Explanation of original labelling: Z.A = adoral zone of membranelles, B = buccal lip, Ma = macronuclear nodule, V.C = contractile vacuole. Page 502.

likely, they have been disposed. I did not check whether or not these slides are still available. Anyhow, since the New York Variety (= *U. mobilis americanus*)[1] is not

[1] In addition to that problem, the type locality of the New York variety is not known (see occurrence).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the nominotypical variety (*U. mobilis mobilis*) the slides could not serve as neotypes for *U. mobilis*. Calkins (1929, p. 63) made various stains (iron haematoxylin, neutral red, methylene blue) of *Uroleptus halseyi*; as in the New York variety it is unknown whether or not (usable) permanent slides are still available. Any way, these methods are inappropriate to reveal details of the infraciliature. In addition, a fixation of *U. halseyi* as type of *E. mobilis* would contradict the issue whether these two species are valid species or synonyms.

(v) There is strong evidence that the population described by Foissner (1982) is consistent with the original description (Engelmann 1862), especially as concerns size, shape, nuclear apparatus, and habitat. Of course we will never exactly know whether or not these populations belong to the same species because Engelmann (1862) did not describe the infraciliature in detail and made not comment about the cortical granules.

(vi) The original type locality is a brook near Prague, Czech Republic (Engelmann 1862; details see occurrence and ecology). Foissner (1982) found *E. mobilis* in a riverine floodplain in Lower Austria, that is, a limno-terrestrial habitat only about 250 km south-east of the original type locality. Consequently, the new type locality is very near the original one, as requested by Article 75.3.6 of the ICZN (1999).

(vii) The protargol slides containing the neotype material are deposited in the Upper Austrian Museum in Linz (accession numbers 1981/96 and 1982/55; see Aescht 2008, p. 166).

The next step is to isolate a population from or very near the type locality of *U. halseyi*. Of course the morphological data have to be supplemented by a comparison of gene sequences.

Remarks: Engelmann (1862) found this slender species with two marginal rows and six macronuclear nodules in a brook. He compared it with the *Uroleptus* species described in great detail by Stein (1859) and simultaneously stated that he could not ascertain whether or not two longitudinal rows of fine ventral cirri, which are characteristic for the uroleptids, are present because of the vigorous movement. According to Engelmann (1862), *U. mobilis* is 300 µm long on average. Interestingly, Kahl

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← **Fig. 86d–m** *Engelmanniella mobilis* (d, from Calkins 1919a, b; e–g, from Calkins 1919b; h, i, from Calkins 1919a; j–m, from Calkins 1929. d–i, m, *Uroleptus mobilis* New York variety; j–l, the synonym *Uroleptus halseyi*; d–m, after fixation and staining). **d, m:** Right or right-ventrolateral view of normal specimen (d = 171 µm, m = 157 µm) showing, inter alia, flattening of anterior body portion, dorsal position of contractile vacuole, and nuclear apparatus (macronuclear nodules with replication band). **e–g:** Specimens degenerated through old age (313–316th generations; same magnification as [d]). Degeneration comprises, inter alia, reduction of size and degeneration of macronuclear nodules and disappearance of micronuclei (f). **h:** Oral area showing frontal cirri, adoral zone, and undulating membrane (endoral; or buccal lip?) right of proximal portion of adoral zone. **i:** Cross-section through anterior region near cytostome of a conjugating specimen, diameter of cell about 16 µm. **j:** Cortical granules (= peripheral excretory granules according to Calkins 1929, p. 68) in posterior end of a specimen killed 24 h after treatment with ultraviolet rays for 30 s (40 µm). **k:** Right ventro-lateral view (185 µm) showing, inter alia, that the contractile vacuole is near the dorsal margin. **l:** Ventral view of a specimen killed 10 min after treatment with ultraviolet rays for 30 s, 112 µm. AZM = adoral zone of membranelles, CV = contractile vacuole, DB = dorsal bristles, FC = frontal cirri, MA = macronuclear nodule, MI = micronucleus. Page 502.

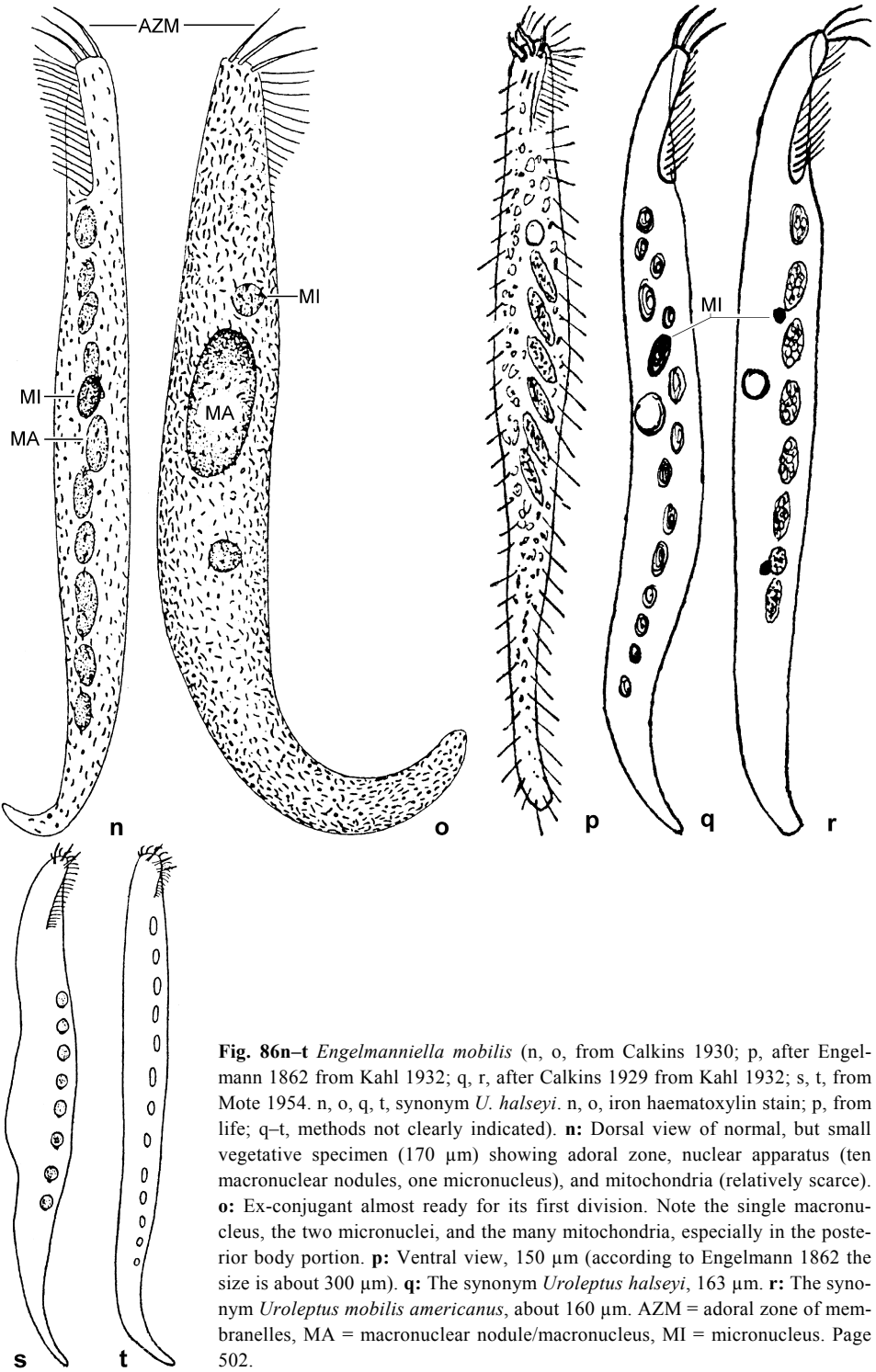


Fig. 86n–t *Engelmanniella mobilis* (n, o, from Calkins 1930; p, after Engelmann 1862 from Kahl 1932; q, r, after Calkins 1929 from Kahl 1932; s, t, from Mote 1954. n, o, q, t, synonym *U. halseyi*. n, o, iron haematoxylin stain; p, from life; q–t, methods not clearly indicated). **n:** Dorsal view of normal, but small vegetative specimen (170 µm) showing adoral zone, nuclear apparatus (ten macronuclear nodules, one micronucleus), and mitochondria (relatively scarce). **o:** Ex-conjugant almost ready for its first division. Note the single macronucleus, the two micronuclei, and the many mitochondria, especially in the posterior body portion. **p:** Ventral view, 150 µm (according to Engelmann 1862 the size is about 300 µm). **q:** The synonym *Uroleptus halseyi*, 163 µm. **r:** The synonym *Uroleptus mobilis americanus*, about 160 µm. AZM = adoral zone of membranelles, MA = macronuclear nodule/macronucleus, MI = micronucleus. Page 502.

(1932) mentioned a length of 85–250 µm in the text and 150 µm as length for the specimen illustrated by Engelmann (1862; Fig. 86p); he provided no explanation, but obviously he assumed that Engelmann has distinctly overestimated the size.

Roux (1901) mentioned and illustrated some isolated ventral cirri along body midline (Fig. 86c; difficult to recognise in illustration, which is very delicate). Very probably these are not uroleptid midventral cirri because Roux also illustrated *Uroleptus musculus* with distinct midventral cirri, indicating that his *U. mobilis* lacks such a pattern. The wide distance between the cirri suggests that these are widely spaced parental cirri, although their location in cell midline is unusual because the central body portion is free of cirri (Foissner 1982, Wirnsberger-Aescht et al. 1989). Thus, we have to assume that Roux (1901) made a misobservation because the cirral pattern of slender species is very difficult to recognise in detail without protargol impregnation. Anyhow, the six obliquely arranged macronuclear nodules strongly indicate that Roux (1901) observed the same species as Engelmann (1862). Like the type population described by Engelmann (1862), the population studied by Roux (1901) was very large (350–400 µm); either both workers made incorrect measurements or their limnetic populations were indeed very large.

Calkins (1919a, 1929) described the so-called New York variety of *Uroleptus mobilis* and *Uroleptus halseyi* because they differed from *U. mobilis* in body size and length:width ratio, number of macronuclear nodules, position of contractile vacuole, and shape of posterior body portion (Table 29). However, the detailed studies by Foissner (1982) and Wirnsberger-Aescht et al. (1989, 1990) strongly suggested that these differences do not allow such a separation (Table 28). Populations from North America, that is, from/near the type locality of *Uroleptus halseyi* have to be studied for a final decision. At present I follow Wirnsberger-Aescht et al. (1990, p. 47), who supposed that the New York variety and *U. halseyi* are only ecological or cultured variants of *E. mobilis*. In spite of the high resemblance, some authors, including European ones, found both *U. mobilis* and *U. halseyi* during the same investigation (e.g., Mote 1954, Biczok 1955, Detschewa 1972, Detcheva 1992, Szabo 1995).

Calkins studied various aspects of *U. mobilis* and *U. halseyi* in detail, inter alia, the nuclear cycle during cell division and conjugation (see reference section). The illustration provided by Grandori & Grandori (1934, p. 284, Tavola XIII, fig. 273) is from Calkins.

Kahl (1932) established *U. mobilis americanus* for the New York variety described by Calkins (1919a, 1929; see nomenclature). In addition, he considered both *U. mobilis* and *U. halseyi* as valid species. Since the cirral pattern was not exactly known at that time, the assignment to *Uroleptus* was only tentatively.

The illustrations of the Iowa populations studied by Mote (1954) are minimalistic and therefore did not provide further insight into the species problem discussed above (Fig. 86s, t). Borror (1972) accepted all taxa of the *Uroleptus mobilis* group (*U. mobilis*; *U. halseyi*; *U. americanus* = New York variety), but recognised that they do not belong to *Uroleptus* because he listed them at the end of his paper, to-

gether with many other taxa in a chapter dealing with species of questionable systematic position. This opinion was also hold by Hemberger (1982, p. 278). Simultaneously, Foissner (1982) redescribed *U. mobilis* demonstrating that it lacks the characteristic midventral cirral pattern of the uroleptids. Likely mainly because of this finding, he removed it from *Uroleptus*, and since it could not be placed in another genus, Foissner (1982) correctly established a new genus (*Engelmanniella*) to which he also assigned *U. halseyi* (at present a junior synonym of *E. mobilis*, see above) and *Uroleptus kahli* Grolière, 1975. However, the latter species was already fixed as type of *Perisincirra* by Jankowski (1978), a small group of hypotrichs which is characterised by primarily widely spaced cirri (further details, see p. 463).

Wirnsberger-Aescht et al. (1989, 1990) studied, inter alia, the cell division, the ultrastructure, the cyst, and the intra- and interpopulational variability of four populations and therefore contributed significantly to the knowledge of this species. They came to the conclusion that *E. mobilis*, the New York variety, and *U. halseyi* are synonymous (see above). Although there is little doubt about this synonymy, at least at the present state of knowledge, the data are kept separate so that the review can even be used by workers who reject this synonymy.

Foissner (1982) was uncertain about the correct designation of the cirri on the posterior end of the cell, and Dragesco (2003) described an African population with 3–5 caudal cirri (Fig. 93a–f, Table 28). Wirnsberger-Aescht et al. (1989) found, during the investigation of the cell division, that caudal cirri are lacking, that is, without the analysis of relevant dividers it is practically impossible to decide unequivocally whether or not a slender species has caudal cirri. Thus, I preliminary suppose that Dragesco (2003) has misinterpreted marginal cirri and/or frontoventral cirri as caudal cirri. Of course one cannot exclude that African populations with caudal cirri exist. Thus, further populations from the same area should be studied.

There exists a rather large number of slender, roughly worm-like limnetic and terrestrial hypotrichs resembling *E. mobilis*, for example, *Uroleptus* (mainly limnetic; distinct uroleptid midventral complex composed of zigzagging ventral cirri present; for brief review, see Foissner et al. 1991), *Uroleptoides* (one left and one right marginal row and one median cirral row present; for review, see Berger 2008, p. 224), *Hemisincirra* (two marginal rows and one short frontoventral row present; for review, see Berger 2008, p. 387), *Perisincirra* (all cirri widely spaced; see p. 463), or *Circinella* (adoral zone less than 10% of body length; p. 309). In vivo, *Engelmanniella mobilis* is relatively easily identified by the following combination of features: very slender body with more or less distinct tail; body length about 150–300 µm; 6–26 medium-sized macronuclear nodules left of midline; about 17 longitudinal rows of colourless to yellowish cortical granules about 0.5 µm across; widely spaced cirri near cell margin; movement sluggish winding, almost like an eelworm.

Chaudhuri (1929) provided a rather simple illustration showing a relatively slender hypotrich with about seven macronuclear nodules (Fig. 95b). I classify it as insufficient redescription (p. 545).

Morphology: The population described by Foissner (1982) is now the neotype of *E. mobilis* and thus reviewed separately. In addition, the original descriptions of the New York variety (Calkins 1919a, 1929) and *U. halseyi* (Calkins 1929) are kept separate in case of the synonymy proposed by Wirnsberger-Aescht et al. (1990) and accepted in the present review turns out wrong. Subsequently, some deviating and/or additional observations from other populations are mentioned below.

Population studied by Foissner (1982; = neotype population; Fig. 87a–f, Table 28): Body size about 170–270 × 18–23 µm; length:width ratio of live specimen illustrated about 10:1, on average 9.3:1 in protargol preparations (Table 28). Body only anteriorly slightly flattened dorsoventrally and thus pronouncedly vermiform. Anterior end narrowly rounded, posteriorly more or less distinctly tapered and almost always curved leftwards; sometimes twisted by half a turn about main body axis (Fig. 87a, b). On average eight macronuclear nodules in middle body portion left of midline, often connected by fine threads; individual nodules in life about 8.0 × 3.5 µm, with many small chromatin bodies. Micronuclei in life about 5.0 × 2.8 µm, compact, strongly refractive (Fig. 87a, e). Contractile vacuole slightly to distinctly ahead of mid-body near left cell margin, during diastole with two long collecting canals (Fig. 87b). Pellicle colourless, flexible. Cortical granules colourless to yellowish, about 0.5 µm across, arranged in about 17 longitudinal rows; granules very conspicuous at high magnification (Fig. 87b). Cytoplasm colourless, packed with tiny, about 1.5 µm

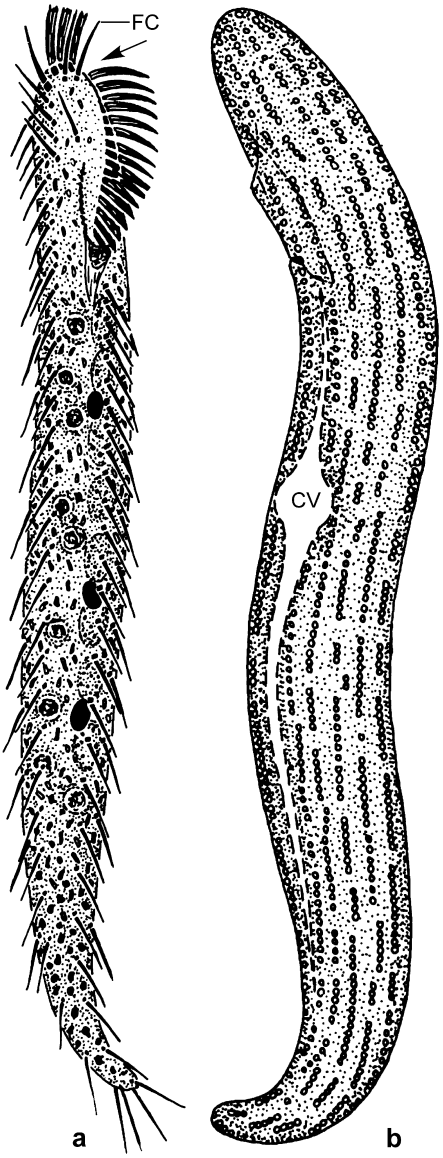


Fig. 87a, b *Engelmanniella mobilis* (from Foissner 1982. Neotype population from life). **a:** Ventral view of a representative specimen, 230 µm. Arrow marks gap in adoral zone. **b:** Dorsal view showing arrangement of cortical granules (colourless to slightly yellowish, about 0.5 µm across, arranged in about 17 longitudinal rows) and contractile vacuole, 172 µm. CV = contractile vacuole with collecting canals, FC = left frontal cirrus. Page 502.

long roods and few to many, about 1.2 µm large, crystalline granules, which are sometimes abundant in posterior body portion. Food vacuoles about 5 µm across, with indefinable content. Movement sluggish, wriggling between plant remains, at low magnification easily confused with a nematode.

Adoral zone of membranelles in life about 35 µm long, in protargol preparations only occupying 16% of body length on average; composed of 3–4 frontal (distal) membranelles separated from proximal portion (on average composed of about 18 membranelles) by distinct gap; proximal portion of zone obliquely extending backwards (details on adoral membranelles, see ultrastructure; Table 28). Buccal field narrow and flat, covered by buccal seal (see below). Paroral[1] very short, that is, composed of only about five cilia, arranged more or less left of buccal cirrus. Endoral straight, distichous, commences somewhat behind paroral, ends at buccal vertex. Pharyngeal fibres short (Fig. 87a, c, d).

All cirri very fine, but posterior one still finer than anterior (further details see ultrastructure). Bases of cirri parallelogram-shaped, about 0.4–0.7 µm in size. Frontal cirri arranged in horizontal pseudorow, right cirrus usually slightly larger than middle and left cirrus which are narrowly spaced and very close to or almost in gap of adoral zone (Fig. 87c–f; see, however, ultrastructure). Buccal cirrus more or less immediately right of the very short paroral (see above). 1–4, usually three parabuccal cirri behind right frontal cirrus; row usually ends about at level of buccal cirrus. Frontoterminal cirri, postoral ventral cirri, pretransverse ventral cirri, and transverse cirri lacking; posterior body end with some unspecific cirri which could not be clearly assigned (marginal, transverse, caudal) by Foissner (1982), obliquely splayed out in life. From the ontogenetic data by Wirnsberger-Aescht et al. (1989) it is known that these are marginal cirri. Invariably three long cirral rows right of midline (frontoventral row, parental right marginal row with widely spaced cirri, normal right marginal row). Frontoventral row commences about at level of first or second parabuccal cirrus, extends to near cell end, composed of about 34 normally spaced cirri on average (for foundation of designation [frontoventral row or inner right marginal row] see remarks at genus section). Next row, that is, parental right marginal row ventrolaterally arranged, rather variable, that is, composed of 5–25, on average 14 widely spaced cirri because they are retained from the previous generation. Right marginal row dorsolaterally arranged, more or less bipolar, composed of 27 normally spaced cirri on average. 2–3, on average 2.1 left marginal rows. Innermost row, obviously the ordinary left marginal row, commences at buccal vertex, extends to rear cell end, composed of 27 normally spaced cirri. Middle left marginal row composed of 11 widely spaced cirri close to left cell margin, retained from parental generation. Outermost left marginal row rarely, that is, in two of 13 specimens pre-

[1] Note that Foissner (1982) confused paroral and endoral in *E. mobilis* and some other species, for example, *Gonostomum affine* (see Fig. 18h in Foissner 1982). Wirnsberger-Aescht et al. (1989, their Fig. 2, 4) also incorrectly labelled the short paroral immediately left of the buccal cirrus as endoral. However, the endoral is in the buccal cavity, underneath the buccal seal (see Foissner & AL-Rasheid 2006). The structure of the paroral (composed of few, relatively widely spaced basal bodies) is reminiscent of *Gonostomum*.

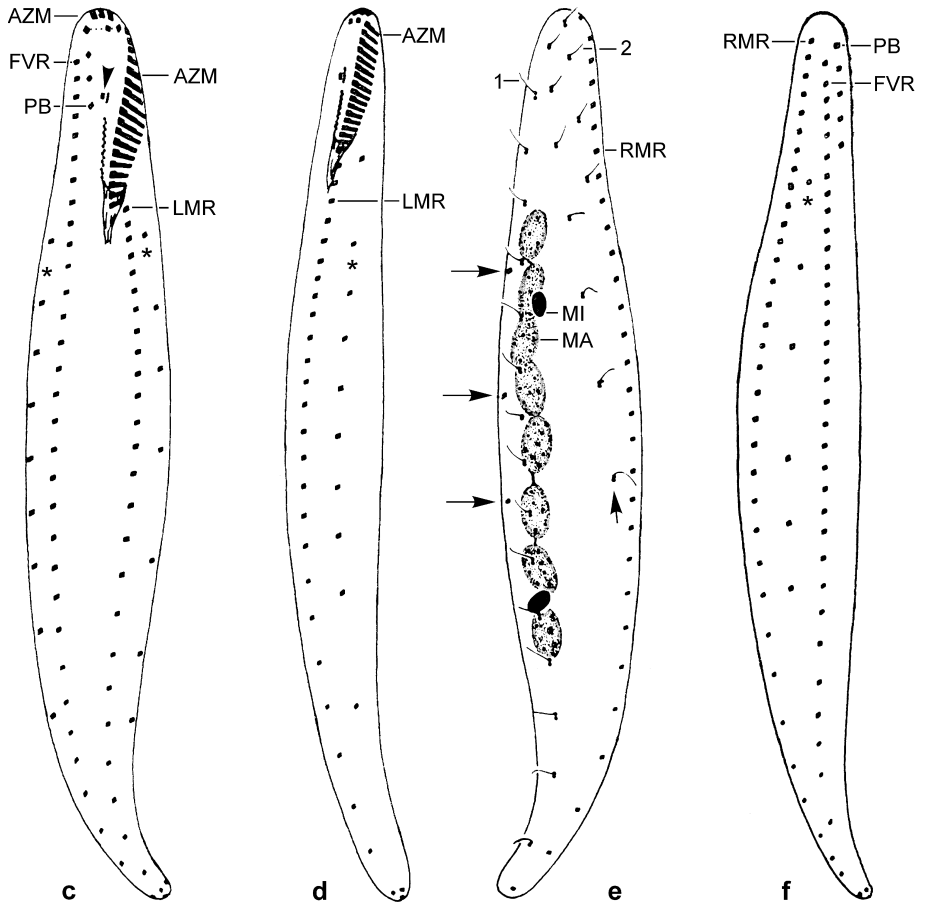


Fig. 87c–f *Engelmanniella mobilis* (from Foissner 1982. Neotype population after protargol impregnation). **c:** Infraciliature of ventral side, 100 µm. Arrowhead marks buccal cirrus right of paroral. **d:** Infraciliature of left side, 124 µm. **e:** Infraciliature of dorsal side, 105 µm. Long arrows mark grandparental left marginal row. Short arrows marks rear end of an additional short dorsal kinety only rarely present. **f:** Infraciliature of right side, 101 µm. AZM = bipartite adoral zone of membranelles, FVR = frontoventral row, LMR = (normal) left marginal row, MA = macronuclear nodule, MI = micronucleus, PB = parabuccal row, RMR = right marginal row, 1, 2 = dorsal kineties 1 and 2, * = parental marginal rows. Page 502.

sent according to Foissner (1982), arranged on dorsolateral surface and confined to middle body third, composed of five or six very widely spaced cirri of grandparental generation. A re-examination of the neotype material by Wirnsberger-Aescht et al. (1990, p. 31), however, revealed that Foissner (1982) has overlooked the grandparental cirri on the left side in most cases; that is, grandparental left marginal cirri are lacking only in about 10% of the specimens.

Dorsal bristles about 4 µm long, usually arranged in two kineties (Fig. 87e). Kinety 1 more or less bipolar. Kinety 2 commences near anterior end, terminates about

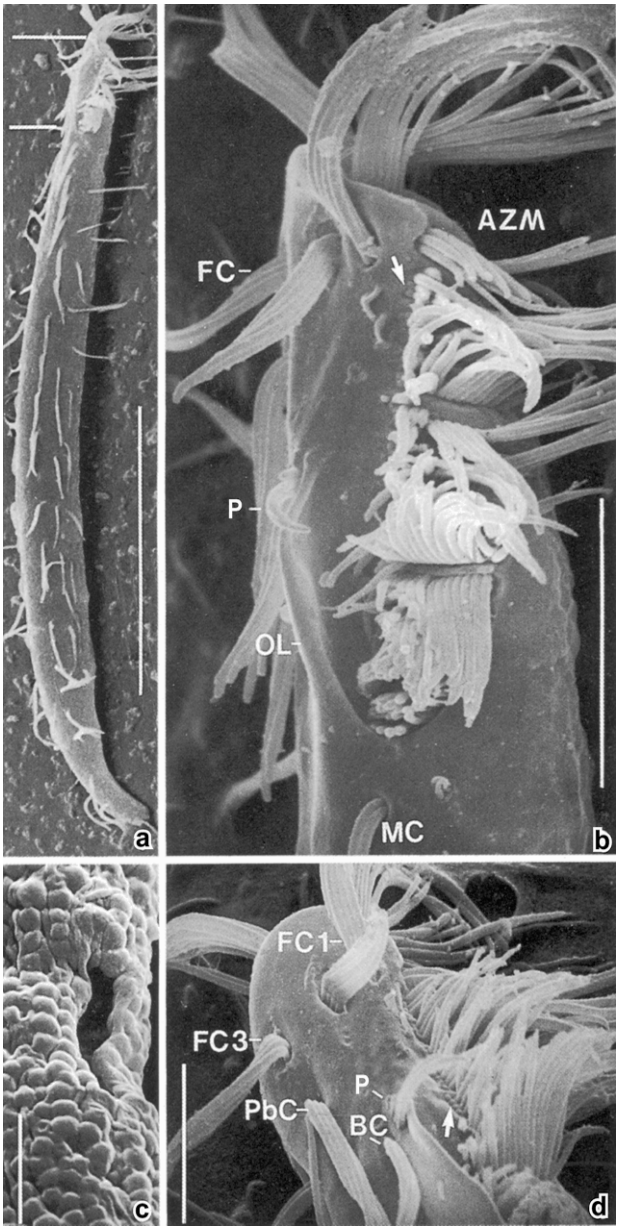


Fig. 88a–d *Engelmanniella mobilis* (a, b, from Foissner 1987a; c, d, from Wirnsberger-Aescht et al. 1989. Scanning electron micrographs of Baumgarten population). **a:** Ventral view showing, inter alia, cirral rows and short oral apparatus (white lines). **b:** Detail of oral apparatus. Arrow marks ciliary stubs of the rightmost basal bodies of the adoral membranelles (see also d). Note the short paroral (incorrectly designated as endoral by Wirnsberger-Aescht et al. 1989); the buccal cavity is covered by the buccal seal and thus the endoral is not recognisable (see also Foissner & AL-Rasheid 2006). **c:** Pore of contractile vacuole on dorsal side. The cortical granules appear as hemispherical elevations in this slightly shrunken cell. **d:** Anterior end of cell showing, inter alia, frontal ciliature (for explanation of arrow, see [b]). The anteriormost parabuccal cirrus is composed of six cilia. Explanation of original labelling (except of paroral): AZM = bipartite adoral zone of membranelles, BC = buccal cirrus, FC = right frontal cirrus, FC1, FC3 = left and right frontal cirrus, MC = left marginal row, OL = buccal lip, P = paroral (see text), PbC = anterior end of parabuccal row. Scale bars: a = 70 µm, b = 10 µm, c, d = 5 µm. Page 502.

in mid-body. Very rarely a kinety 3 is present. Caudal cirri lacking. For variability of dorsal kinety pattern, see next paragraph.

Wirnsberger-Aescht et al. (1990) compared the morphology of four populations (Austria, Baumgarten; Austria, Grafenwörth; Turkey; Japan) and found a more or less identical in vivo aspect. A morphometric comparison demonstrated that the vari-

ability among populations is greater than that within populations. A comparison with the NNSD method (Berger et al. 1985) showed that the two Austrian populations and the Turkish population are rather similar, while the Japanese is distinctly separated (Table 28). The population from Japan had a wider body, a larger adoral zone, and more cirri in the marginal rows. Wirnsberger-Aescht et al. (1990) also compared specimens from the non-flooded Petri dish method (natural population) and cultured specimens. Interestingly, the extreme values of the length of the adoral zone and the number of adoral membranelles and the number of cirri in the frontoventral row did not overlap in the natural and cultured populations from Turkey (Table 28). The cultured specimens were distinctly larger than those from the natural population (average body length 222 µm vs. 135 µm; Table 28). A similar phenomenon was found in the number of micronuclei. About 30% of the specimens from the natural Turkish population had a single micronucleus, whereas cultured cells from the same site had about four micronuclei like the Japanese population (Fig. 91b, d). Wirnsberger-Aescht et al. (1990) found specimens with 1–3 dorsal kineties. The short kinety (= kinety 2), usually composed of 3–6 bristle complexes, is frequently reduced to a single pair or even lost in two thirds of cultured Japanese specimens, a feature never observed in the Austrian and Turkish populations. Some further details on variability, see Wirnsberger-Aescht et al. (1990).

New York variety described by Calkins (1919a; = *Engelmanniella mobilis americana*; Fig. 86d–i, m, r, Table 29): Body size of fixed interphasic specimens[1] 140–168 × 11–17 µm, on average 158 × 15 µm; length:width ratio about 10.5:1. Body shape constant, tapering gradually to broadly pointed posterior end, which is curved towards ventral side. Body supple, circular in cross-section, except for adoral zone area which is distinctly flattened dorsoventrally (Fig. 86d). Eight macronuclear nodules in left body portion; macronuclear nodules of specimen shown in Fig. 86d with replication bands; only one out of many hundred specimens had six macronuclear nodules, whereas 9–12 nodules were found more frequently than six. 2–6 minute, homogenous micronuclei at variable positions. Contractile vacuole about in mid-body near dorsal side. Cytoplasm dense and alveolar with few granules. According to Calkins (1919a), refractive granules form heavy cortical layer; they are globular during interphase, but are drawn out into rods, which divide transversely during division stages. This statement indicates that Calkins mixed up cortical granules and mitochondria, both of which are close beneath the pellicle and have a similar size (Wirnsberger-Aescht et al. 1989). Adoral zone occupies about 17% of body length, roughly rectangularly shaped; specimen illustrated (Fig. 86h) with about 17 membranelles. Buccal field very inconspicuous, with "narrow" undulating membrane right of proximal portion of adoral zone, that is, Calkins (very likely) observed the relatively long endoral (cp. Fig. 86h). Three frontal cirri arranged in oblique pseudorow; anteriormost cirri of rows conspicuous giving impression of five or six frontal cirri in total. Calkins illustrated a cross-section of a conjugant and con-

[1] According to Calkins (1919a, Table on p. 296) division stages have a body length of 93–115 µm (average 99 × 30 µm) and conjugation stages measure 85–120 µm (105 × 15 µm).

cluded that three rows of ventral cirri are present, and that they are finer and shorter than the marginal cirri, which are long, distinct, and sparsely distributed along straight rows, indicating that he saw, at least partially, the parental rows with the widely spaced cirri.

Synonym *Uroleptus halseyi* as described by Calkins (1929, Fig. 86j–l, n, o, q, Table 29): As discussed above, *U. halseyi* is very likely a synonym of *E. mobilis*. The most important differences, according to Calkins (1929), are summarised in Table 29. In addition, Calkins provided the following data: body form constant, plastic; body circular in cross section; body length:width ratio about 9:1, but ratios up to 16:1 have been observed; body size highly variable, obviously dependent upon the age of the culture and nature of the medium; posterior body end tapering gradually to form a long sharp tail distinctly curved towards the ventral side, curvature of tail much more pronounced than in either of the other forms; body much more worm-like than in New York variety, twists and doubles on itself in all directions as it forces its way into *Zoogloea* masses or detritus. Adoral zone ("peristome") well marked and more conspicuous than in New York variety occupying one sixth to one seventh (14–17%) of body length. Cortical granules ("excretory granules") arranged in longitudinal rows. According to Calkins (1930a), the micronucleus is the most important feature separating *U. mobilis* and *U. halseyi*. While *U. mobilis* has 2–6 micronuclei, *U. halseyi* has typically never more than two. The micronuclei of *U. halseyi* are very large, often as large as the macronuclear nodules. However, due to its homogenous structure it cannot be mistaken as a macronuclear nodule, although it often forms a chain with the macronuclear nodules. The micronuclei are spherical or ellipsoidal, stain readily with iron haematoxylin and react positive with the Feulgen method (Calkins 1930a).

In this paragraph data of the old descriptions are summarised. Engelmann (1862) provided the following data (Fig. 86a, b): body length in life 300 µm on average, most specimens of same size; length:width ratio about 12:1. Body supple, holds its shape; circular in cross section; bluntly pointed posteriorly. Six serially arranged, oblong macronuclear nodules. Adoral zone occupies about one ninth of body length; buccal field very small. Engelmann (1862) could not ascertain whether or not two longitudinal rows of fine ventral cirri are present because specimens lively mobile and snake-like creeping among rotting plants. Specimens described by Roux (1901, Fig. 86c) in life 350–400 × 40 µm. Body contractile, cylindrical, especially in central portion. Six ellipsoidal, askew lying macronuclear nodules arranged one after the other behind the contractile vacuole. Contractile vacuole at 33% of body length in specimen illustrated. Three distinct frontal cirri. No buccal cirrus illustrated, indicating that Roux has overlooked it. Some isolated ventral cirri, illustrated specimen with about nine. 49 cirri in frontoventral row; about 40 cirri in inner left marginal row. Further measurements: body length 85–250 µm (Kahl 1932); 155–290 µm (Luzzatti 1938); 320 µm (Grispini 1938). For details on Rwandan population described by Dragesco (2003), see Fig. 93a–f and Table 28.

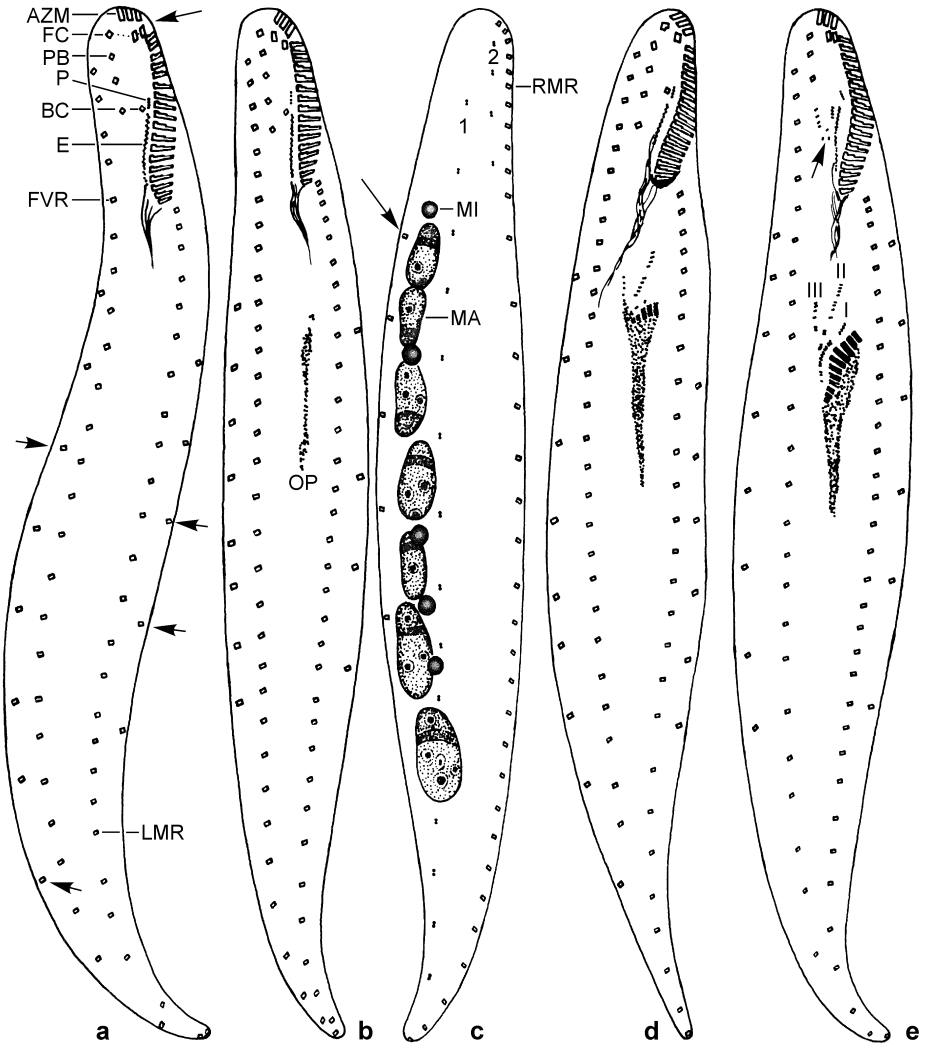


Fig. 89a–e *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1989. Protargol impregnation of Baumgarten population). **a:** Infraciliature of ventral side of interphasic specimen, 120 µm. Short arrows mark parental cirri, which are rather widely spaced. Long arrow denotes gap in adoral zone. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of very early divider, 133 µm. Arrow in (c) marks grandparental left marginal cirri. The longitudinal oral primordium develops de novo. Each macronuclear nodules has a replication band. **d, e:** Infraciliature of ventral side of early dividers, d = 121 µm, e = 120 µm. In the opisthe three anlagen (I–III) originate from the oral primordium. In the proter the buccal cirrus modified to anlage II while some rear parabuccal cirri form anlage III. Probably some basal bodies originate de novo (arrow in e). AZM = distal end of adoral zone of membranelles, BC = buccal cirrus, E = endoral, FC = frontal cirri, FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, OP = oral primordium, P = paroral, PB = parabuccal row, RMR = right marginal row, I–III = frontal-ventral cirri anlagen I–III, 1, 2 = dorsal kineties 1, 2. Page 502.

Cell division (Fig. 89a–q): Morphogenesis of cell division of *E. mobilis* was studied in detail in the Baumgarten population by Wirnsberger-Aescht et al. (1989; for summaries, see Wirnsberger et al. 1987 and Foissner 1996, p. 105). Generally, the formation of the new ciliature proceeds relatively simply, inter alia, because the ciliature is rather strongly reduced. Wirnsberger-Aescht et al. (1990) studied cell division in a Turkish and Japanese population and could basically confirm their previous results.

Stomatogenesis. The oral primordium originates apokinetally, that is, without contact to parental structures close to mid-body (Fig. 89b). It broadens anteriorly and the three distal membranelles are formed (Fig. 89d, e). In the proter, the anlage for the left frontal cirrus (anlage I) originates from the parental paroral. The parental endoral is slightly disordered in later dividers, indicating that it is also reorganised, at least partially (Fig. 89h). Wirnsberger-Aescht et al. (1989) found that the new parental paroral originates in the usual way, that is, by an anterior longitudinal splitting in the endoral. The parental adoral zone is retained for the proter; however, the pharyngeal fibres are invisible in later ontogenetic stages, indicating that they are reorganised (Fig. 89k, o).

Formation of frontoventral and marginal cirri. In the opisthe the frontoventral cirri anlagen I–III originate from the oral primordium (Fig. 89d, e). In the proter, anlage I originates from the undulating membranes; anlage II from the buccal cirrus; and anlage III from the 2–4 rearmost parabuccal cirri. Perhaps in some specimens some basal bodies originate de novo (Fig. 89e, arrow). Wirnsberger-Aescht et al. (1990) studied this part in detail in two other populations and confirmed the composite origin of anlagen II and III, that is, partly de novo, partly from the buccal cirrus and the posterior parabuccal cirri. Somewhat later each two primordia occur within the parental right marginal and the left marginal row (Fig. 89f, g). Just in the next stage two primordia are formed within the parental frontoventral row (Fig. 89h), indicating that this is not a marginal row, but part of the frontoventral ciliature. No anlagen occur within the old marginal rows, which are easily recognisable on the widely spaced cirri (Fig. 89f–k). The posterior portion of the marginal row anlagen migrate backwards right to the parental row, that is, the old marginal rows are shifted leftwards both on the right and the left side of the cell[1]. Between the newly formed right marginal and the newly formed frontoventral row usually one row of widely spaced old (= parental) cirri is present. By contrast, left of the newly formed left marginal row two old rows (parental and grandparental) are present. This process was termed neokinetal wave by Eigner (1995, p. 343, 361). The transverse splitting of the remaining parental and grandparental marginal rows on two daughter cells, together with the elongating cell cortex, causes the distances among parental and grandparental rows to be wider than those in the newly formed marginal rows (Fig. 89h–q). The “grandparental” right marginal row and the “great-grandparental”

[1] In some illustrations one has the impression that the old rows are on the right side of the new marginal rows (e.g., Fig. 89l–n); however, this is an optical artefact because the parental rows are actually not on the dorsal side as the new row, but on the ventral side.

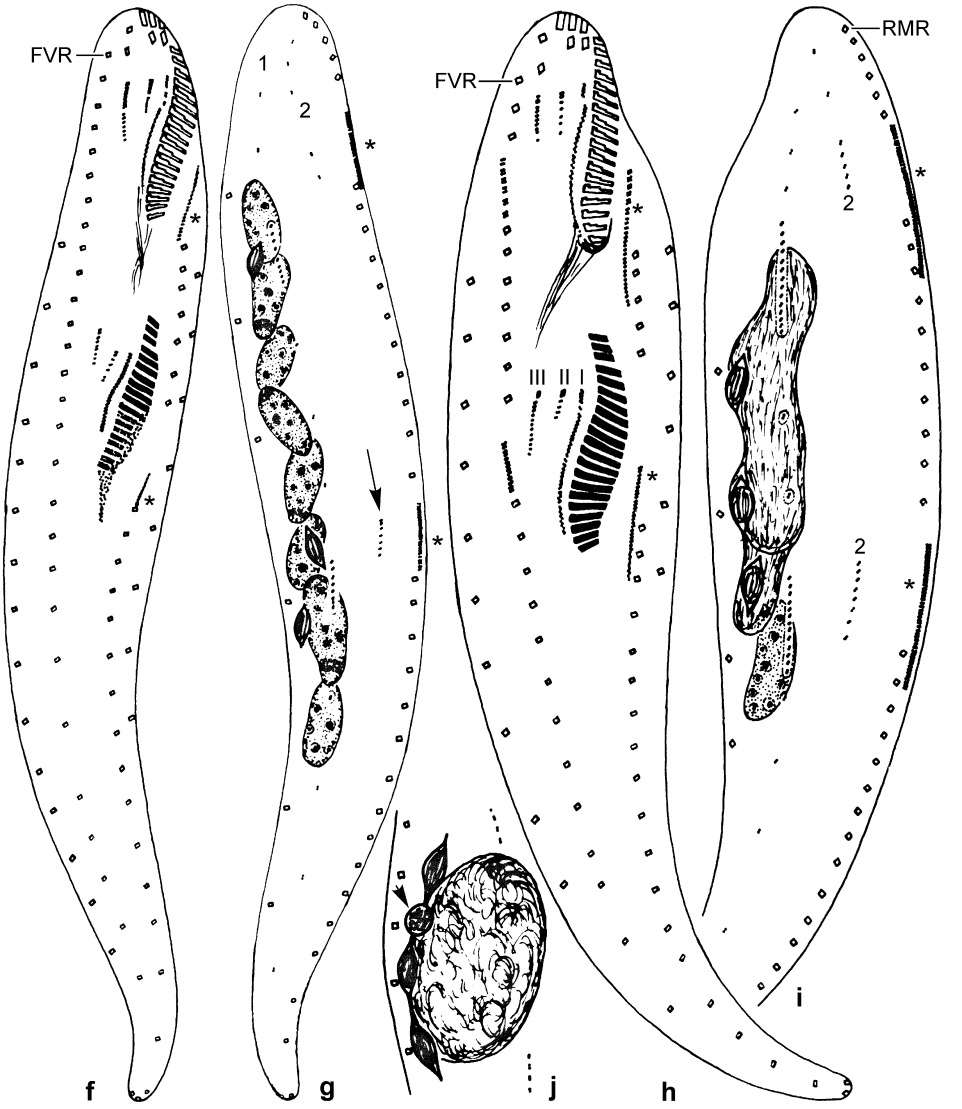


Fig. 89f–j *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1989. Protargol impregnation of Baumgarten population). **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of middle divider, 125 µm. The paroral of the proter has modified to anlage I and the anlagen for the marginal rows have formed within the parental marginal rows (asterisks). Note that within the frontoventral, designated as inner right marginal row by Wirnsberger-Aescht et al. (1989), anlagen are not yet recognisable. The arrow in (g) marks the apokinetal origin of dorsal kinety 2 of the opisthe. **h, i:** Infraciliature of ventral and dorsal side and nuclear apparatus of middle divider, 130 µm. Asterisks mark anlagen within marginal rows. Within the parental frontoventral row two anlagen have formed, one for the proter and one for the opisthe. The macronuclear nodules have fused to a single mass and the micronuclei became prophasic. **j:** The macronuclear mass condenses, some micronuclei do not divide (arrow). FVR = frontoventral row, RMR = right marginal row, I–III = frontal-ventral cirri anlagen I–III, 1, 2 = dorsal kineties. Page 502.

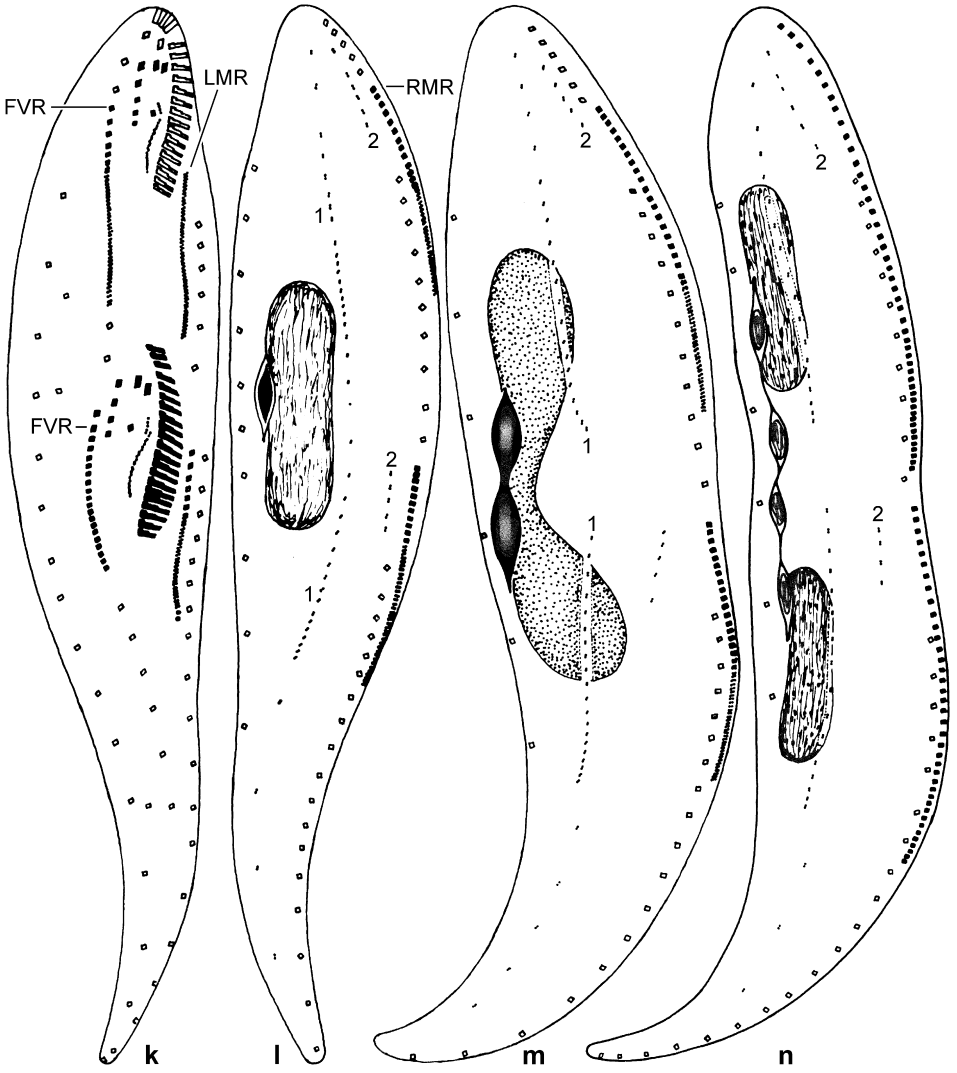


Fig. 89k–n *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1989. Protargol impregnation of Baumgarten population). **k, l:** Infraciliature of ventral and dorsal side and nuclear apparatus of late divider, 112 µm. Note various generations (four on right side, three on left) of marginal rows. **m, n:** Infraciliature of dorsal side of late dividers showing division of nuclear apparatus. Several micronuclei are covered with a single envelope. FVR = frontoventral row, LMR = new left marginal row of proter, RMR = new right marginal row of proter, 1, 2 = dorsal kineties 1 and 2. Page 502.

left marginal row, the parental frontoventral row, the frontal cirri, and one or two parabuccal cirri are resorbed (Fig. 89k, o). Wirnsberger-Aescht et al. (1990) found that grandparental left marginal cirri are invariably present in the Baumgarten population (Austria) and the Japanese population (natural and cultured). Grandparental

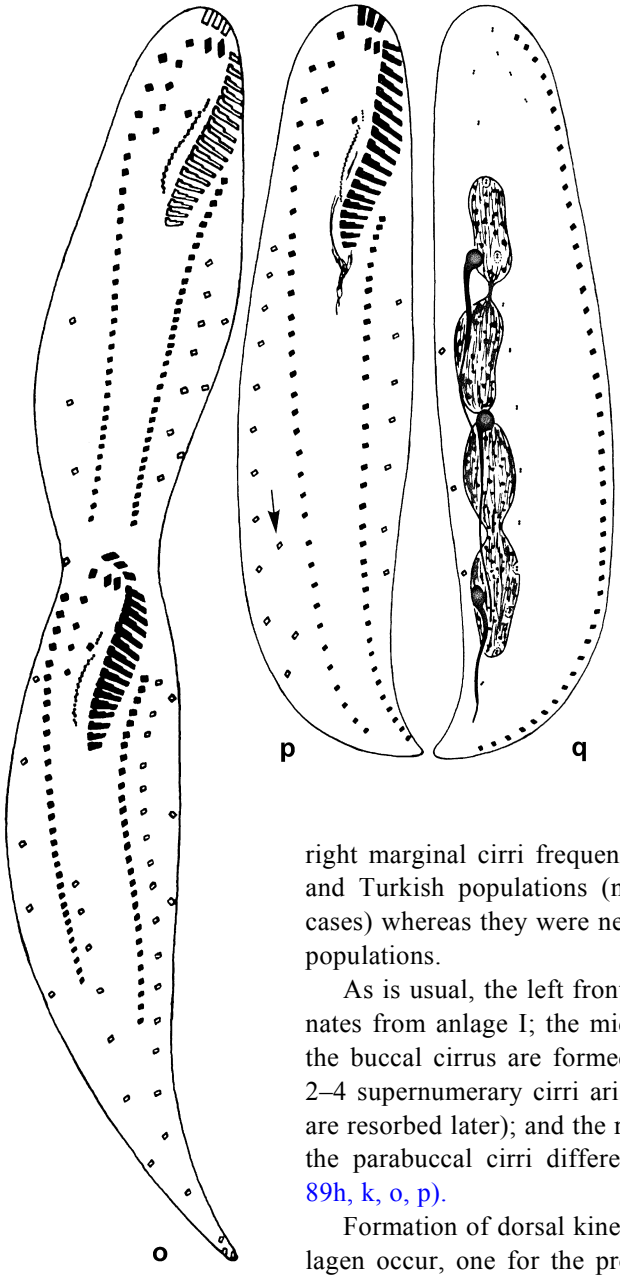


Fig. 89o–q *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1989. Protargol impregnation of Baumgarten population). **o:** Infraciliature of ventral side of very late divider, 127 µm. Note that the parental and grandparental cirri are not resorbed after division, a feature reminiscent of the kahliellids. **p, q:** Infraciliature of ventral and dorsal side and nuclear apparatus of postdivider, 67 µm. Arrow marks a short grandparental right marginal row. According to Wirnsberger-Aescht et al. (1989), this is a proter; the black adoral membranelles, however, indicate that it is the opisthe with the newly formed adoral membranelles. Page 502.

right marginal cirri frequently occurred in the Japanese and Turkish populations (natural and cultured in both cases) whereas they were never observed in the Austrian populations.

As is usual, the left frontal cirrus (= cirrus I/1) originates from anlage I; the middle frontal cirrus (II/3) and the buccal cirrus are formed from anlage II (frequently 2–4 supernumerary cirri arise in this primordium which are resorbed later); and the right frontal cirrus (III/3) and the parabuccal cirri differentiate from anlage III (Fig. 89h, k, o, p).

Formation of dorsal kineties. Within kinety 1 two anlagen occur, one for the proter and one for the opisthe (Fig. 89g, i, l–n). The short dorsal kinety 2, on average composed of four bristles only, originates apokinetally in the opisthe. By contrast, kinety 2 of the proter is formed from the rear end of the parental row. Parental dorsal kinety structures are resorbed after the new bristles have moved to their final positions. No caudal cirri are formed. Dorsomarginal kineties and kinety fragmentation are lacking.

Division of nuclear apparatus. The nuclear behaviour is to a certain extent independent from the development of the cortical pattern (Wirnsberger-Aescht et al. 1989). In about 50% of the individuals, the fusion of the macronuclear nodules is completed just when the frontal anlagen are formed whereas in the other half the fusion occurs when the new cirri are differentiated or even during their final displacement. The macronuclear nodules show, as is usual, replication bands before any cortical divisional processes occurs (Fig. 89c, g). After the passage of the band, the nodules fuse to an irregularly shaped mass showing a fibrous content, and further condensations results in an elliptical mass with whirling fibres (Fig. 89i, j). The ordinary number of macronuclear nodules is restored by subsequent divisions (Fig. 89l–n, q). Wirnsberger-Aescht et al. (1989) found that only some micronuclei divide, because relatively often (14%, n = 29) only a spindle-like micronucleus or two yet connected micronuclei were present (Fig. 89l, m), although the non-dividers had at least two micronuclei. Non-dividing micronuclei are not recognisable in late dividers. However, among 68 relevant dividers micronuclear ghosts could not be detected. In addition, the Baumgarten population sometimes (7%; n = 55) produces a chain of three to four micronuclei enclosed in a single envelope (Fig. 89n). Later stages, however, seem to be quite normal, that is, had telophasic micronuclei (Fig. 89q). Wirnsberger-Aescht et al. (1990) found a "single micronucleus stage" only in 2% of the relevant stages (n = 153) in the Japanese population. Further, no micronucleus-chain enclosed in a single envelope was recorded in 178 dividing Japanese specimens, but 37% (n = 238) contained 1–3 interphasic micronuclei, and even in the latest dividers they were found in 23% of the Japanese specimens, indicating that some of the micronuclei might be transferred to the post-dividers. The Turkish specimens studied by Wirnsberger-Aescht et al. (1990) had a similar nuclear cycle as the Baumgarten population, except for the chain-formation.

Further details on division of the nuclear apparatus, see Calkins (1919a, 1926, 1930, 1930a, 1934), Belar (1926, p. 172), and Geng et al. (1992).

Ultrastructure: The ultrastructure of *E. mobilis* was studied in great detail by Wirnsberger-Aescht et al. (1989; for summary see Wirnsberger et al. 1987). Here only some details are briefly mentioned, that is, the interested reader is referred to the original publication containing, inter alia, 27 transmission, scanning, and freeze-fracture photomicrographs. The ultrastructure of the cyst was investigated by Wirnsberger-Aescht et al. (1990; see below).

The pellicle of the ventral and dorsal side is usually multilamellate consisting of 3–6 three-layered membranes, while other areas of the cell are covered by up to 17(!) such membranes (Fig. 90a–c). Close to the cirri, the pellicle is composed of two membranes, probably an external perilemma and the cell membrane. The alveoli are indistinct in ultrathin section (Fig. 90c). Below the somatic pellicle is, as in other flexible hypotrichs (e.g., *Oxytricha*, Grimes 1972) a single layer of longitudinal subpellicular microtubules enclosed by the inner alveolar membrane and a cytoplasmic membrane (Fig. 90a–c).

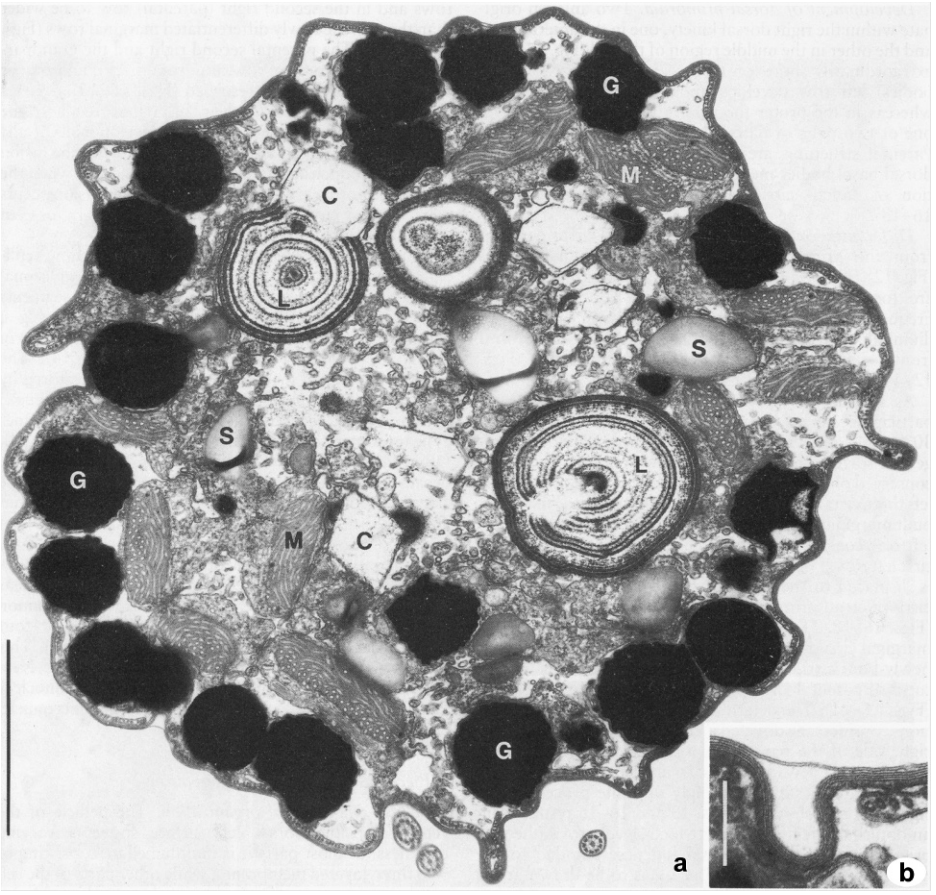


Fig. 90a, b *Engelmanniella mobilis* (from Wirnsberger et al. 1989. Transmission electron microscopy). **a:** Cross section in the middle region of the cell. **b:** Transverse section of a structure probably corresponding to the pellicular invaginations shown in Fig. 28 and 29 in Wirnsberger-Aescht et al. (1989). Explanation of original labelling: C = crystal-like structures, G = cortical granules, L = lithosomes, M = mitochondria, S = starch grains. Scale bars: a = 3 µm, b = 200 nm. Page 502.

The cortical granules are about 0.5–1.0 µm across (Fig. 87b, 90a, d), causing a distinctly wrinkled surface in suboptimal critical-point dried cells (Fig. 88c). According to Wirnsberger-Aescht et al. (1989), they are not extrusive during the interphase because (i) no empty granules were found electron-microscopically (Fig. 88c, 90a); (ii) no anchoring rosettes (Hausmann 1978) could be observed in freeze-fracture replicas; (iii) they do not stain with alcian blue; and (iv) heat, methyl-green pyronin, acetone, and various other regents caused no extrusion. The granules, which are covered by a membrane, are colourless to slightly yellow in the light microscope, but very dark stained by the electron-microscopical procedures and silver

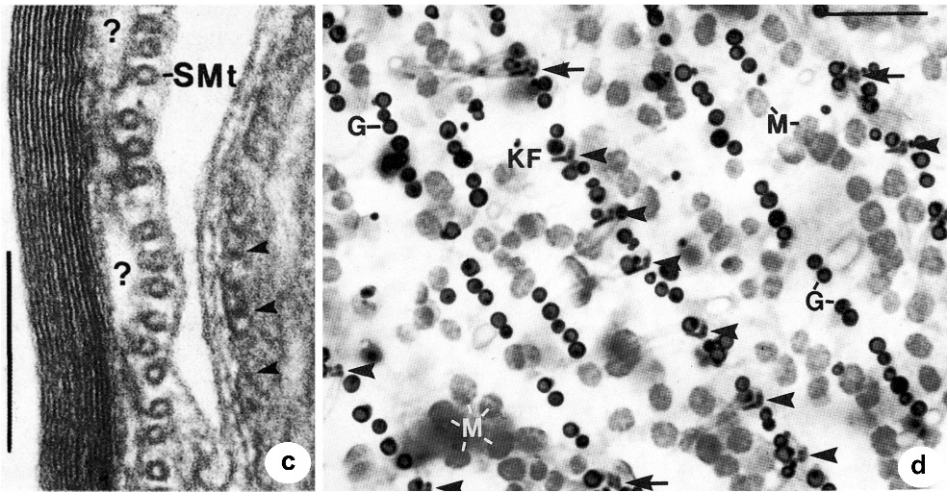


Fig. 90c, d *Engelmanniella mobilis* (from Wirnsberger et al. 1989. c, transmission electron microscopy; d, silver carbonate impregnation). **c:** Multilamellate pellicle accompanied by the alveoli (?) and a single layer of subpellicular microtubules. Regularly patterned mitoribosomes (arrowheads) are visible on the inner side of the mitochondrial membrane. **d:** Detail of ventral side. The marginal cirri are composed of four basal bodies (arrows) in the anterior region, while they consist of two basal bodies (arrowheads) in the posterior third of the cell. Note the rows of the argyrophylic cortical granules and numerous mitochondria. Explanation of original labelling: G = cortical granules, KF = kinetodesmal fibre, M = mitochondria, SMt = subpellicular microtubules. Scale bar 200 nm. Page 502.

carbonate (Fig. 90a, d). The granules are strongly osmiophilic, show a slightly Feulgen positive reaction, and their lamellar structure during development indicates that they contain complex lipids. Wirnsberger-Aescht et al. (1989) also described the putative developmental stages of the granules. Interestingly, the cortical granules are absent from the pellicle and the cytoplasm of encysted cells indicating that they contribute to the formation of the cyst wall (see below).

The left frontal adoral membranelles are composed of four rows of basal bodies, while the right one is made of only three (Fig. 90e); likely only two of them bear cilia. The membranelles of the proximal portion of the zone consist of four rows, except of the proximalmost one, which is made up of only two rows. According to Wirnsberger-Aescht et al. (1989), the paroral is invisible in scanning electron micrographs obviously because it is covered by the buccal lip (Fig. 88b). However, as already mentioned above, Wirnsberger-Aescht et al. (1989) mixed up endoral and paroral, and the endoral is invisible in scanning electron micrographs mainly because covered by the buccal seal (Foissner & AL-Rasheid 2006, p. 5). Probably the endoral is made up of a single row of basal bodies; however in silver carbonate preparations a second row of unciliated basal bodies is sometimes recognisable. 3–4 µm long immobile structures emerge from the basal bodies of the endoral; whether these are cilia or nematodesma could not be decided (Wirnsberger-Aescht et al. 1989).

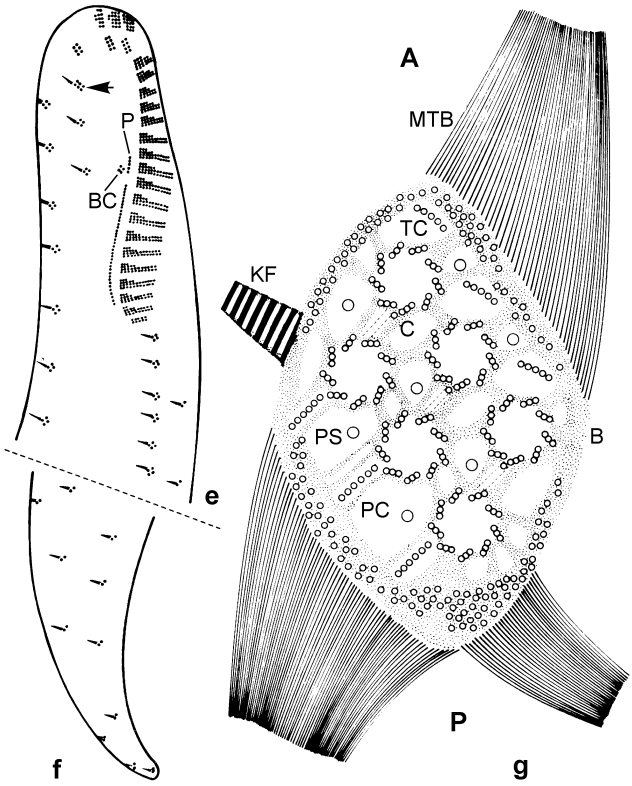


Fig. 90e–g *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1989). Diagrams of the infraciliature. The number of basal bodies comprising the oral and somatic ciliature is rather constant. Arrow in (e) marks anteriormost parabuccal cirrus. The microtubular and microfibrillar associates of which are shown in (g). A = anterior, B = basket, BC = buccal cirrus, C = electron-dense connections, KF = kinetodesmal fibre, MTB = microtubular bundle, P = paroral (e) or "posterior" (g), PC = postciliary microtubulus, PS = parasomal sac, TC = transverse microtubules. Page 502.

The paroral is left or slightly ahead of the buccal cirrus and composed of 3–7 about 6–7 µm long cilia (Fig. 87c, 88b, d, 89a, 90e). Their basal bodies probably bear only postciliary microtubules.

The cirri of *Engelmanniella mobilis* are made up of the following number of basal bodies/cilia: left and middle frontal cirrus, 8–10; right frontal cirrus, six;[1] buccal cirrus and anteriormost parabuccal cirrus, 4–6; other parabuccal cirri, four; marginal cirri of youngest generation (that is, ordinary marginal cirri), usually four in anterior two thirds and two in posterior third; parental and grandparental marginal cirri, usually two. All cirri are ciliated and show the same basic organisation as in other hypotrichs. Notwithstanding, their structure is strongly reminiscent of dikinetids because all basal bodies form pairs each showing a transverse and a postciliary microtubular ribbon, that is, the cirri of the *E. mobilis* consist of groups of paired basal bodies and simple dikinetids surrounded by a typical cirral basket (Fig. 90e–g).

The dorsal bristle complex of *E. mobilis* is almost identical to that of other hypotrichs, as for example, *Kahliella*, *Paraurostyla*, *Laurentiella*, and *Oxytricha* (Fleury et al. 1985, Grimes & Adler 1976, Jerka-Dziadosz 1982, Torres et al. 1986; for re-

[1] Foissner (1982) found that the right frontal cirrus is often larger than the left and middle one.

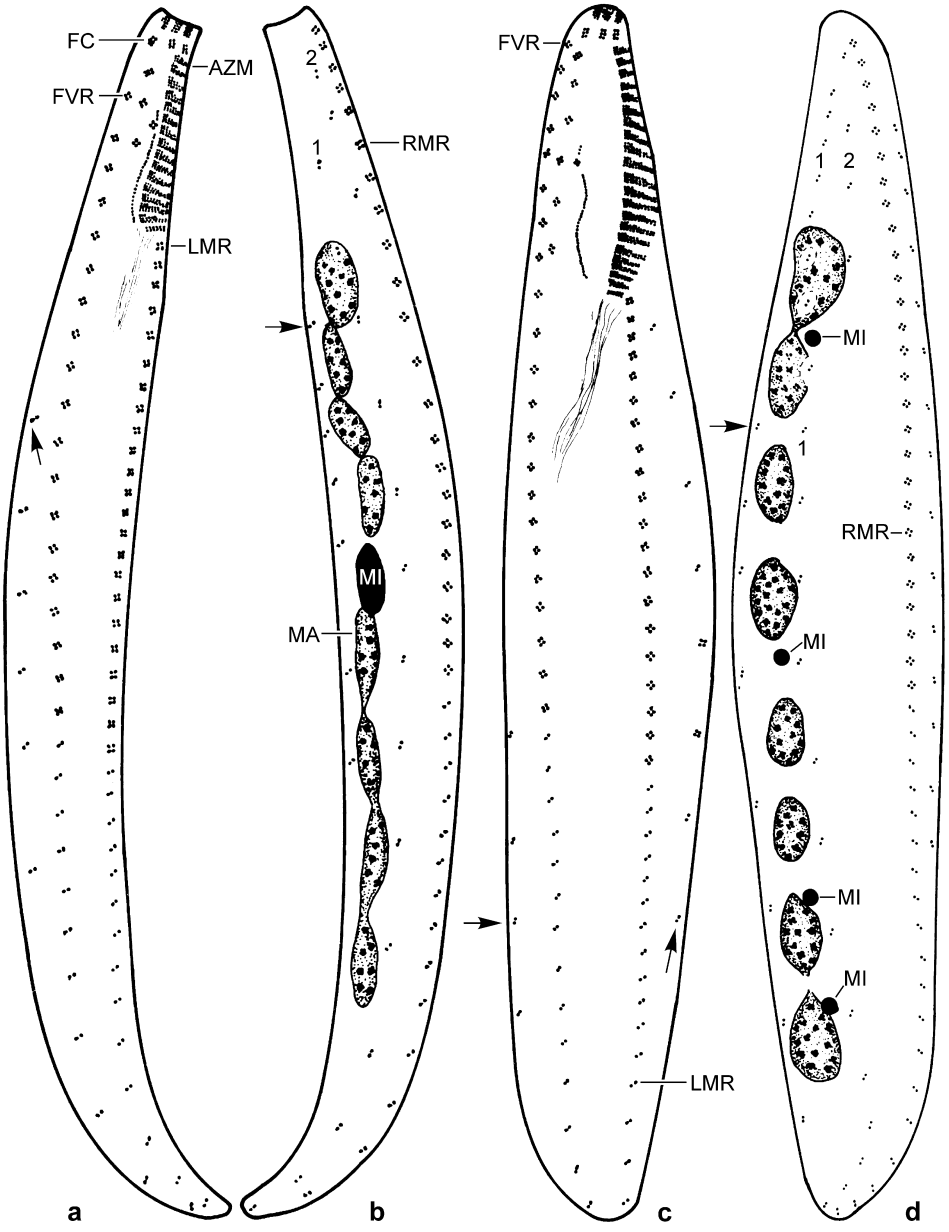


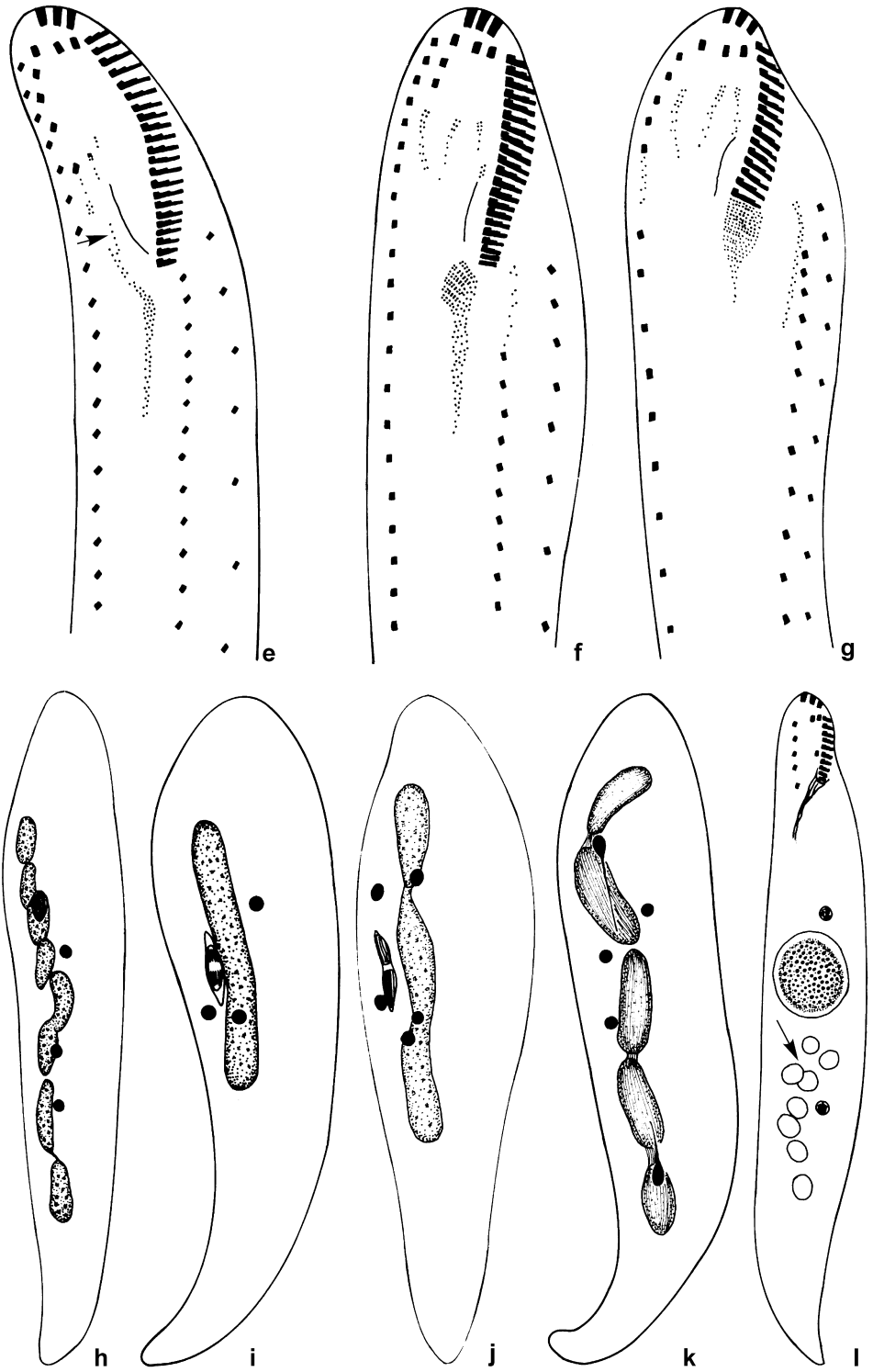
Fig. 91a–d *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1990. Protargol impregnation). Infraciliature of ventral (a, c) and dorsal (b, d) side and nuclear apparatus of Turkish (a, b) and Japanese population (c, d). Note the distinct gap in the adoral zone. Arrows mark parental and grandparental marginal cirri. FC = right frontal cirrus, FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RMR (outer) right marginal row, 1, 2 = dorsal kineties. Page 502.

view, see Berger 1999). According to Wirnsberger-Aescht et al. (1989), the dorsal bristle complex can be distinguished from the paired basal bodies of the cirri by the following features: (i) only the anterior basal body of a dorsal bristle complex is ciliated; (ii) possession of only a proximal interkinetosomal connective; (iii) the electron dense material surrounding the pair is asymmetrically arranged; (iv) the microtubules originating from this material are relatively few in number and short; (v) the absence of the kinetodesmal fibre, a structure also lacking in the stylonychine *Laurentiella* (Torres et al. 1986; Lynn 1991, p. 126).

Reorganisation (Fig. 91e–l): This part of the life cycle was studied by Wirnsberger-Aescht et al. (1990) in the populations from Austria (Baumgarten), Turkey, and Japan, and was mainly found in well-nourished cultures and, to a less extent, in the raw material. The process proceeds, as is usual, similar to that in dividers. The undulating membranes are completely replaced and only 6–8 newly formed adoral membranelles join with the posterior portion of the parental zone, where several membranelles have been resorbed (Fig. 91f, g). Contrary to cell division, the nuclear cycle of reorganisers is correlated with cortical processes. In 28 reorganisers, Wirnsberger-Aescht et al. (1990) found only rarely (in two or three cases) a replication band in one of the macronuclear nodules, indicating that no reorganisation of the macronucleus takes place, as already supposed by Jerka-Dziadosz & Frankel (1970) in *Paraurostyla weissei*. Further details on reorganisation, see Wirnsberger-Aescht et al. (1990).

Conjugation: According to Calkins (1919a), this part of the life cycle invariably preceded by a characteristic massing or agglomeration of specimens. These masses varied in size from about 3–6 mm across containing thousands of individuals very closely packed together. Conjugation lasts about 28–36 h. Calkins (1919a, 1930, 1930a) mainly studied the nuclear apparatus during conjugation in great detail; the reader is therefore referred to these papers and the review by Bělar (1926, p. 147). The macronuclear nodules remain independent, lose their staining capacity, and disappear in the cytoplasm (Calkins 1930). In postconjugating specimens, the nodules fuse to a single mass in the central body portion (Foissner 1982).

Calkins (1919b) studied the renewal of vitality through conjugation in the New York variety. The results showed, inter alia, that the physiological processes of metabolism are not able of unlimited activity. The limits varied from the time of conjugation (or excystment) to between 268 and 349 generations by division. Within these limits there was a progressive weakening of metabolic vigor from an optimum shown during the first three months after conjugation. Calkins found the last individuals of a series showed evidences of morphological as well as physiological degeneration. The specimens became distinctly smaller and the micronuclei entirely disappeared, probably by absorption. The macronuclear nodules did not disappear, but showed characteristic changes indicating degeneration. The eight nodules usually remained independent, but showed evidence of an attempt to fuse as they do prior to division in a normal specimen.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Calkins (1920) found that the striking variability in vitality of different clones are due to the age, and therefore to the relative vitality of the parent cells at the time of conjugation. All clones with extremely low vitality agreed in coming from parents which were old when they conjugated, while all series with very high vitality derived from parents which were young at the time of conjugation. Calkins (1921) investigated the effect of cutting during conjugation in the New York variety.

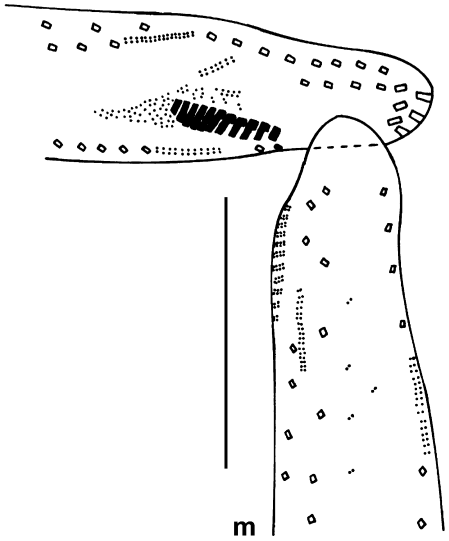


Fig. 91m *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1990. Protargol impregnation of Japanese population). Intraclonal conjugants. The frontoventral anlagen I–III originate from the oral primordium like in the opisthe during cell division. Scale bar = 10 µm. Page 502.

Wirnsberger-Aescht et al. (1990) found several stages of this part of the life cycle in populations from Austria, Turkey, and Japan. The nuclear cycle largely corresponded with that described by Calkins (1919a, b, 1930a, b), with the exception of the number of pronuclei. Calkins found that in *E. mobilis* 8–16 micronuclei became prophasic, whereas in the synonym *U. halseyi* typically never more than two micronuclei entered mitosis. Wirnsberger-Aescht et al. (1990) recorded 2–5 pronuclei in the Japanese specimens and 1–3 in the Turkish. The oral primordium is formed de novo in each conjugant and produces all frontal anlagen, like the opisthe during cell division. Only a small adoral zone is reorganised and paroral and endoral are lacking in exconjugants. A subsequent physiological reorganisation is followed by encystation. Wirnsberger-Aescht et al. (1990) tried to determine the mating-type reactivity of the Turkish and Japanese populations. They found one pair (Fig. 91m), however, they supposed that it was an intraclonal conjugation which occurred several times in one of these definite clones later.

Doublets originate by complete fusion of conjugating specimens (Fig. 94a–c; details see Calkins 1926 and Dogiel 1929, p. 467).

← **Fig. 91e–l** *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1990. Protargol impregnation of Japanese population). **e–k:** Reorganising cells, e = 52 µm, f, g = 60 µm, h = 105 µm, i = 98 µm, j = 84 µm, k = 87 µm. Arrow marks a small streak extending to the frontal area. Further details, see text. **l:** Oral area and nuclear apparatus of an exconjugant, 112 µm. Note the absent undulating membranes, the synkaryon, and the resorbing macronuclear nodules (arrow). Page 502.

Table 30 Morphometric data of resting cysts of *Engelmanniella mobilis* (T, Turkish population; J, Japanese population. From Wirnsberger-Aescht et al. 1990)

Characteristics [a]	Pop	Mean	M	SD	SE	CV	Min	Max	n
Mucus layer, thickness (from life)	T	6.2	6.0	1.7	0.4	26.5	4.0	10.0	21
	J	–	–	–	–	–	–	–	–
Diameter (from life)	T	35.5	35.0	3.9	0.7	10.9	29.0	44.0	29
	J	33.4	33.0	3.0	0.5	8.9	26.0	41.0	33
Cyst wall, thickness (from life)	T	2.4	2.5	0.6	0.1	26.3	2.0	4.0	23
	J	1.8	2.0	0.4	0.1	21.0	1.2	3.0	17
Opaque vacuole, diameter (from life)	T	11.9	12.5	1.3	0.4	10.9	10.0	14.0	10
	J	10.5	7.5	1.9	0.5	18.1	7.0	15.0	14
Macronuclear nodules, number	T	1.0	1.0	–	–	–	1.0	1.0	15
	J	1.0	1.0	–	–	–	1.0	1.0	15
Micronuclei, number	T	2.7	3.0	1.2	0.3	43.0	2.0	5.0	15
	J	2.5	3.0	1.1	0.3	42.4	1.0	4.0	15
Micronuclei, length	T	4.1	4.0	1.3	0.3	32.3	3.0	6.0	15
	J	2.9	3.0	1.0	0.3	34.5	2.0	5.0	15
Micronuclei, width	T	3.8	4.0	1.1	0.3	30.0	3.0	5.0	15
	J	2.1	2.0	0.6	0.2	30.7	2.0	3.0	15

[a] All measurements in µm. In vivo measurements comprise natural and cultured cells. Length and width of micronucleus obviously from protargol preparations. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known), SD = standard deviation, SE = standard error of arithmetic mean.

Cyst (Fig. 92a, b, d–h, Table 30): Encystation of *Engelmanniella mobilis* was studied by Wirnsberger-Aescht et al. (1990) from the Turkish and Japanese population. They found a very similar process, but the populations differed in their capability to make cysts and to excyst. Natural and cultured specimens of the Turkish population immediately formed cysts after transfer into fresh medium without food; the cyst formation lasted about 2 d. By contrast, resting cysts of the Japanese population were difficult to obtain, that is, starved specimens rounded up, but many of them failed to produce the cyst wall and died. Encystation of the Japanese cells lasted about 3–4 d. Cysts of both populations air-dried for about one month could be reactivated by adding fresh culture medium and food, however, the Turkish population excysted more quickly than the Japanese.

For a detailed description of the resting cyst, including documentation with photomicrographs, see Wirnsberger-Aescht et al. (1990). Here only a brief description and the morphometric characterisation are given. The cyst wall is either smooth (sometimes with adhering detritus; Japanese populations) or has a distinct mucus envelope with released granules and adherent bacterial endospores (Turkish and Baumgarten populations, see below). Fully developed resting cysts have a single kidney-shaped macronucleus and some yellow opaque inclusions, mostly included in a single vacuole (Fig. 92a, d). The peripheral zone of the finished cyst lacks cortical granules indicating that they have been discharged. Obviously the granules cross the plasma membrane and the developing cyst wall. The cyst wall is of usual structure: a thin

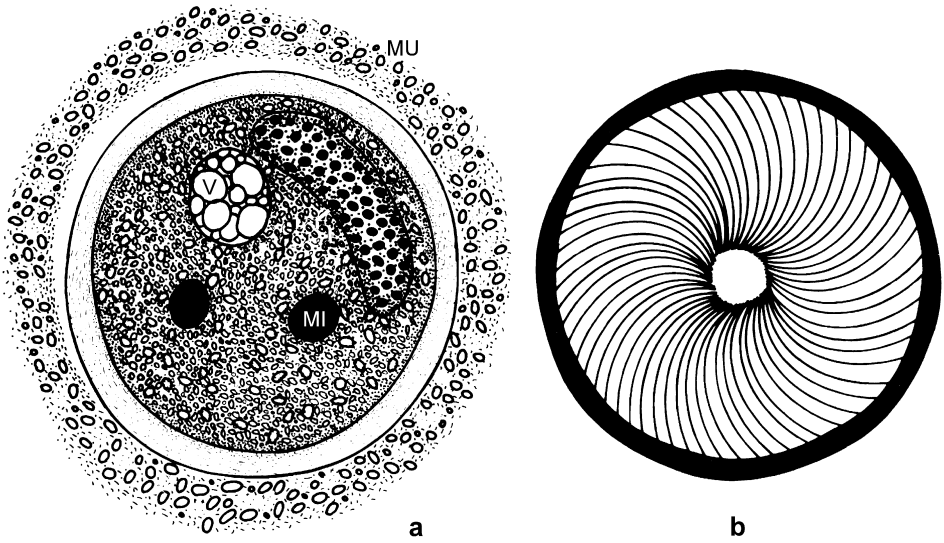
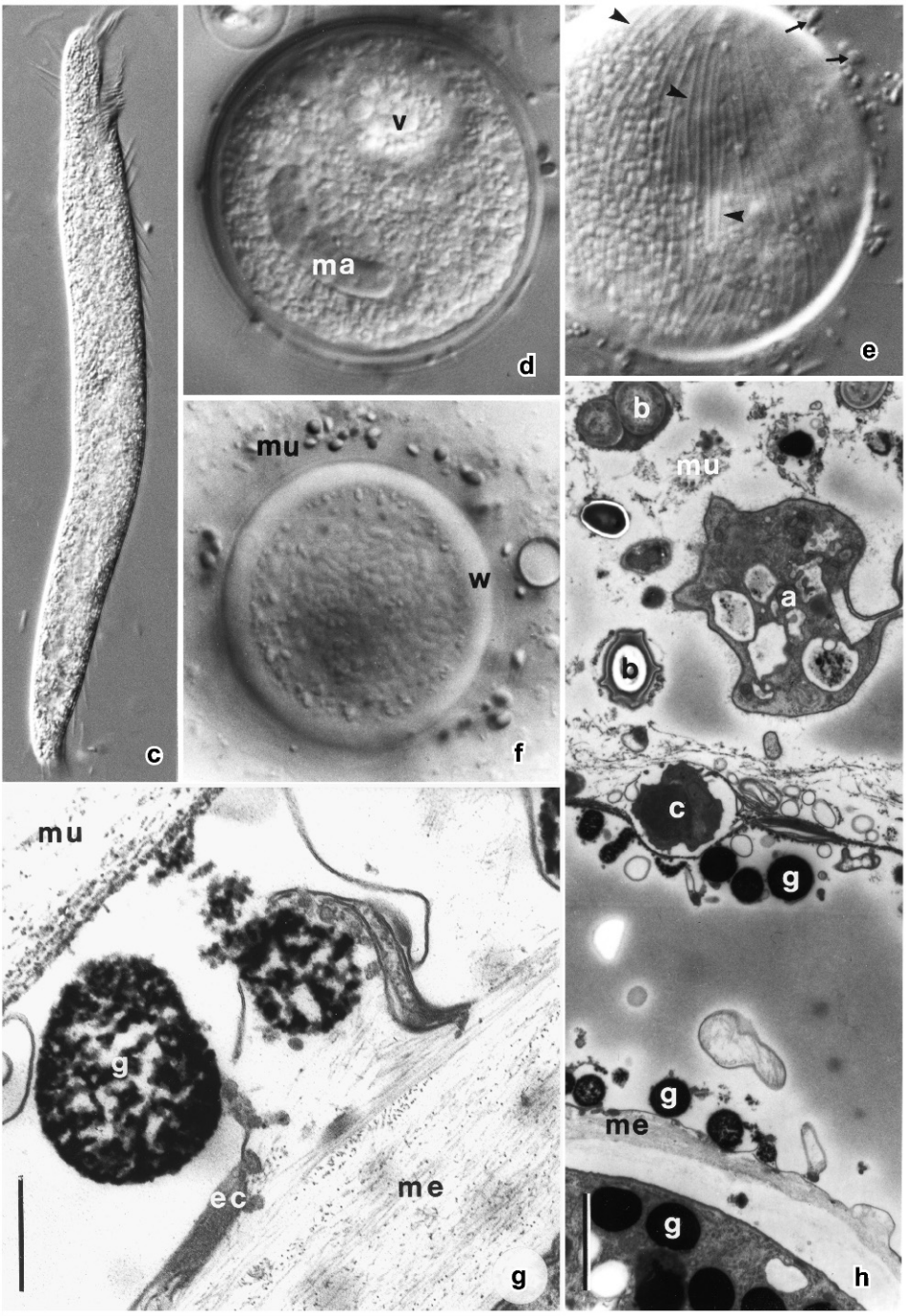


Fig. 92a, b *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1990. Turkish population. From life). **a:** Resting cyst, 46 µm (including mucous layer). The cyst wall is about 2 µm thick, the cytoplasm contains, inter alia, a kidney-shaped macronucleus. **b:** Radially stripes are visible on old and young cysts (see e). Diameter 25 µm. MI = micronucleus, MU = mucous layer with released cortical granules and adhering bacterial endospores, V = single vacuole filled with opaque inclusions. Page 502.

ectocyst; a filamentous mesocyst; an endocyst; and an inner granular layer, filling the rims of the cytoplasmic surface (Fig. 27 in Wirnsberger-Aescht et al. 1990). A single layer of microtubules is located beneath the cell membrane. Mitoribosomes were observed like in the interphasic cells (Wirnsberger-Aescht et al. 1990). Oxytrichid (four-layered cyst wall, fused macronuclear nodules) and urostyloid (cortical microtubules) features are mixed up in the resting cyst wall of *E. mobilis*, similar as in *Kahliella simplex* and *Paraurostyla weissei*, either indicating that the separation in distinct cyst groups is possibly not quite correct (Wirnsberger-Aescht et al. 1990, Martin-Gonzalez et al. 1992) or these taxa branched off between the urostyloids and the oxytrichids.

The resting cyst volume is about 33% of the vegetative cell volume, which is in the range of other hypotrichs (Martin-Gonzalez et al. 1992; Foissner et al. 2006, p. 335). The diameter is 33–35 µm on average (Table 30), which agrees perfectly with the value (32.7 µm; globular; smooth cyst wall) given by Calkins (1919a, p. 296) for the New York variety.

Molecular data: W. Foissner, who redescribed the species in detail (Foissner 1982, Wirnsberger-Aescht et al. 1989, 1990), has identified the population which was analysed by various workers (Hogan et al. 2001, p. 15101; Croft et al. 2003, p. 342; Hewitt et al. 2003, p. 259; Foissner et al., 2004, p. 267); thus, the identification is beyond doubt. There exist several entries in the GenBank: macronuclear SSU rRNA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(AF164134; 1773 bp linear DNA; Prescott et al. unpublished, submitted June 1999); micronuclear actin I gene (AY092778; 1472 bp linear DNA; Hogan et al. 2001); SSU rDNA, ITS 1, 5.8S, ITS 2, 26S (AF508757; 1773 bp, 121 bp, 154 pb, 201 bp, 1375 bp linear DNA; Hewitt et al. 2003); actin-encoding macronuclear DNA, 5' Leader, ORF, 3' Trailer (AY044837; 1437 bp [1477 bp according to GenBank database], 109 bp, 1131 bp, 197 bp; Croft et al. 2003, Hogan et al. 2001); actin I (AAK98784; 376 aa; Hogan et al. 2003, Croft et al. 2003); micronuclear actin I (AAM47498; 376 aa; Hogan et al. 2003).

Engelmanniella mobilis is used in several molecular biological analyses (e.g., Prescott 1998, Stoeck et al. 2003, 2006, Agatha et al. 2005, Coleman 2005, Richards et al. 2005). Hogan et al. (2001) found in a tree comprising only some stylonychines and *Urostyla grandis* the present species in between these two groups (stylonychines, urostyloids), both in a SSU rDNA tree and an actin I gene tree, a position also estimated by Chen & Song (2001) in their Fig. 3. In a more detailed tree, Croft et al. (2003) estimated a position (together with the uncertain *Paraurostyla viridis*; for review, see Berger 2006, p. 1106) between the Dorsomarginalia (roughly: uroleptids + oxytrichids) and the urostyloids using actin molecules. By contrast, in some other trees it clusters close to or even within the oxytrichids (e.g., Croft et al. 2003; Hewitt et al. 2003, their Fig. 3; Hu et al. 2009b). In a third group of trees it clusters with or at least close to *Hemiurosoma terricola* Foissner et al., 2002a, type of *Hemiurosoma* Foissner et al. 2002a (e.g., Foissner et al. 2004, Foissner & Stoeck 2006a). *Hemiurosoma* is, according to Berger (2008, p. 614), a non-oxytrichid dorsomarginalian. Gong et al. (2007) found a close relationship of this *Engelmanniella* + *Hemiurosoma* clade with ((*Oxytricha granulifera* + *Halteria grandinella*) + (*Uroleptus* sp. + (*Cyrtohymena*/*Paraurostyla* + stylonychines))). In the tree published by Foissner & Stoeck (2008), the present species has the following position: (((((((*Rigidothrix goiseri* + *Oxytricha granulifera*) + *Onychodromopsis flexilis*) + *Halteria grandinella*) + *Orthoamphisiella breviseries*) + *Hemiurosoma terricola*) + *Engelmanniella mobilis*) + *Gonostomum* spp.) + (*Uroleptus* spp. + oxytrichids). A similar position was estimated by Li et al. (2008), Sonntag et al. (2008), Li et al. (2009), Paiva et al. (2009), and Yi et al. (2009). Some trees are little expressive (e.g., Shin 2005). In the tree published by Snoeyenbos-West et al. (2002), *E. mobilis* clusters with *Urostyla grandis*, type of the urostyloids. A placement outside the oxytrichids is also indicated by micronucleus actin genes, which are scrambled in the oxytrichids but not scrambled

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← **Fig. 92c–h** *Engelmanniella mobilis* (from Wirnsberger-Aescht et al. 1990. c–f, differential interference contrast micrographs; g, h, transmission electron micrographs). **c:** Ventral view of specimen of Turkish population. **d, e:** Resting cyst of Japanese population lacks a mucous layer. Note the stripes on the surface (arrowheads). **f:** Resting cyst of cultured Turkish population with mucous layer. **g, h:** Young cysts of the Baumgarten population have a mesocyst, but yet lack the endocyst and the granular layer. Some of the extruded cortical granules (g) are swollen and form the mucous sheet (mu) where bacterial endospores (b) and a small amoeba (a) adhere. Explanation of original labelling: a = small amoeba adhering, b = bacterial endospores, c = cytoplasmic material, ec = ectocyst, g = cortical granules, ma = macronucleus, me = mesocyst, mu = mucus layer, v = vacuole with opaque inclusions, w = cyst wall. Page 502.

in *Engelmanniella* and *Urostyla* (Hogan et al. 2001, Jahn & Klobutcher 2002, p. 504, Dalby & Prescott 2004, p. 253, Kim et al. 2004), indicating that the unscrambled state is part of the ground pattern of the hypotrichs (Berger 2008, p. 42). Schmidt et al. (2007) found a close relationship with *Oxytricha lanceolata*, an *Oxytricha* species which lacks a dorsal kinety fragmentation indicating that the assignment to *Oxytricha* is incorrect (for review, see Berger 1999).[1]

As with other hypotrichs, the position of *E. mobilis* is rather variable within various molecular trees and thus details should not be overinterpreted. However, the following rough conclusions can be drawn: (i) *Engelmanniella mobilis* clusters (often) distinctly outside the core oxytrichids which is in agreement with the lack of a dorsal kinety fragmentation, the main morphological apomorphy of the oxytrichids (Berger 2006, 2008); (ii) *Engelmanniella* branches off later than the urostyloids and some other groups (e.g., amphisiellids) lacking a dorsomarginal kinety; *Engelmanniella* has one bipolar kinety and one kinety which is distinctly shortened posteriorly commemorative of a dorsomarginal kinety. Ontogenetic data, however, clearly show that this shortened row is not a dorsomarginal kinety originating from/near the right marginal row anlage as this is the case in *Hemiurosoma terricola*, a species which clusters close to *Engelmanniella* in molecular trees (Wirnsberger-Aescht et al. 1989, Foissner et al. 2002, Berger 2008). At present I do not know a reasonable explanation for these contradictions; perhaps the dorsomarginal kinety was reduced in *E. mobilis* or the molecular analyses are incorrect.

Physiology: Austin (1927) made an attempt to prolong the life cycle of the New York variety. Specimens cultivated in Locke-egg medium made 388 divisions over a period of 401 days, which is an average division rate of about 0.97 per day. Austin made, inter alia, one experiment to test the variation in the life-cycles of four series, all starting from a single specimen. The results showed that lines within a race (i) may respond quite differently to a stimulus, such a subjection to starvation for a short period; (ii) may vary considerably in tendency to conjugate; (iii) may show wide differences in the total number of generations and days attained during life. In

[1] The genus *Oxytricha* comprises likely about 60 valid species (54 according to Berger 1999, p. vii), at least half of them are not described in detail. *Oxytricha* as characterised by Berger (1999, p. 115) is a non-monophyletic group, as indicated, inter alia, by the very different dorsal infraciliature (dorsal kinety 3 fragmentation present vs. absent) and oral apparatus (e.g., *O. siseris*). This unsatisfactory situation is mainly due to the fact that *Oxytricha* lacks an apomorphy, that is, it is almost exclusively defined via plesiomorphies (e.g., flexible body, 18 frontal-ventral-transverse cirri, undulating membranes in *Oxytricha* pattern, caudal cirri present) which are largely already present in the last common ancestor of the hypotrichs (Berger 2006, 2008). Non-monophyly is also indicated by molecular markers, although the trees differ rather distinctly so that details should not be overinterpreted (e.g., Schmidt et al. 2007, Sonntag et al. 2008). *Oxytricha granulifera* (type species) and several other species (e.g., *O. longigranulosa*, *O. nauplia*?, *O. ottowi*, *O. rubripuncta*) have a dorsal kinety 3 fragmentation whereas this feature is obviously lacking in a rather high number of species (e.g., *O. longa*, *O. setigera*, *O. islandica*, *O. lanceolata*). Thus, for these species a new genus has to be established, and other genera, for example, *Actinotricha* for *Oxytricha saltans*, should be reactivated to unravel the rather tricky situation step by step. For the reasons mentioned above (apomorphies lacking or difficult to recognise), "*Oxytricha*" species as defined currently can occur throughout the Dorsomarginalia, provided that they have a dorsomarginal kinety. For authorship and date of species, see Berger (1999, 2001).

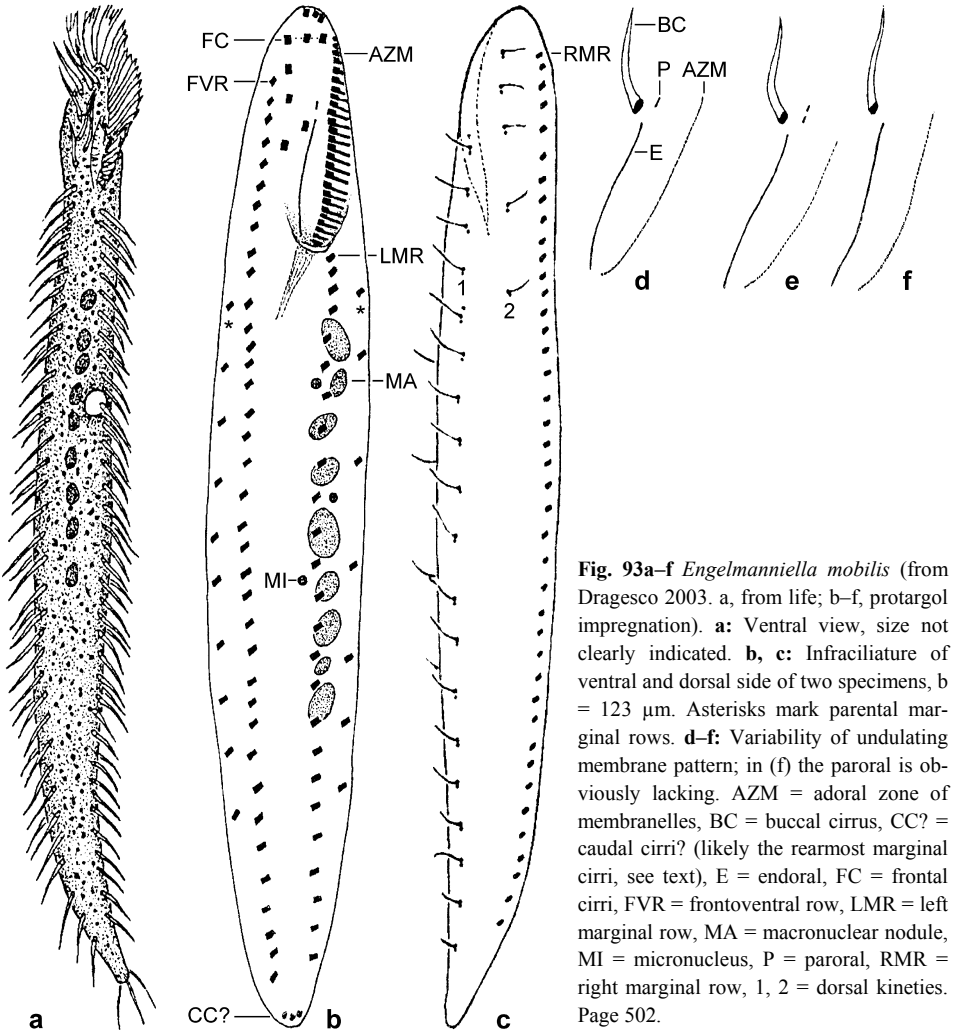


Fig. 93a–f *Engelmanniella mobilis* (from Dragesco 2003. a, from life; b–f, protargol impregnation). **a:** Ventral view, size not clearly indicated. **b, c:** Infraciliature of ventral and dorsal side of two specimens, b = 123 µm. Asterisks mark parental marginal rows. **d–f:** Variability of undulating membrane pattern; in (f) the paroral is obviously lacking. AZM = adoral zone of membranelles, BC = buccal cirrus, CC? = caudal cirri? (likely the rearmost marginal cirri, see text), E = endoral, FC = frontal cirri, FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, RMR = right marginal row, 1, 2 = dorsal kineties. Page 502.

a further experiment, Austin (1927) studied the factors favouring conjugation. She found, inter alia, a great variation in the conjugating power of different races, carried along at the same time and treated in the same way. Further, conjugation occurs within the pH limits 5.2 to 8.6 (in general, a lowering of pH seemed to be more favourable to conjugation than a raising of pH) and accumulation of CO_2 favoured conjugation, but the oxygen content had to be sufficient to maintain the health of the culture (Austin 1927).

Calkins (1929) studied the effect of ultraviolet rays on the synonym *U. halseyi*. He used a Cooper-Hewitt mercury lamp (known as Uviarc) and placed it at a distance of about 23 cm from the surface of the Syracuse dish containing the ciliates in an about 10 mm thick layer of culture medium. Calkins summarised the results as

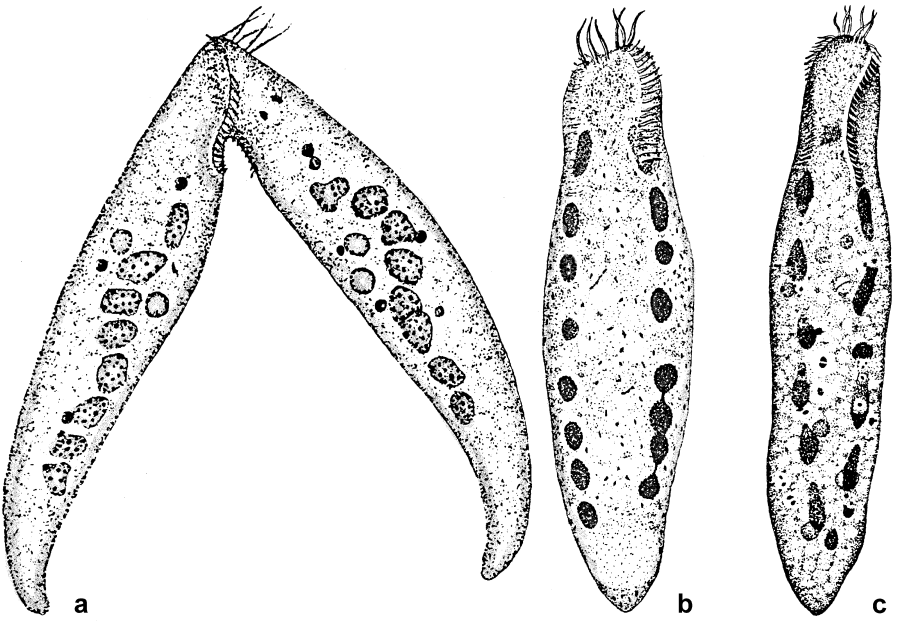


Fig. 94a–c *Engelmanniella mobilis* (from Calkins 1926. After fixation and staining?). **a:** Two conjugating individuals. **b, c:** Double specimens. A doublet is formed by the fusion of a conjugating pair (sizes not indicated); it is easily recognisable by the double adoral zone of membranelles and a double nuclear apparatus. Page 502.

follows: (i) A reduction in size and a change in shape of the cell. (ii) Locomotion was at first normal, but slowed down after 6–8 h. At 48 h the cells were quiet save for movement of the membranelles and at 60 h they were dead. (iii) The mitochondria(?) disappeared immediately after radiation. They collected in granular masses which ultimately turned yellow. (iv) The macronuclear nodules underwent granular degeneration and disintegrated. (v) The micronuclei became elongate and disfigured. (vi) The characteristic Feulgen reaction was given at all stages indicating the nucleic acid persisted throughout. (vii) The cortical granules were enlarged and apparently became more numerous. (viii) An exposure of 30 s to ultraviolet rays produced no monsters. This dosage is lethal to *U. halseyi*, but not lethal to many other types of Protozoa exposed at the same time.

Delamater (1936) studied the effect of heavy water (D_2O) on *E. mobilis*. 0.44% D_2O did not influence the fission rate. A concentration of 48.1% lowered fission rate and lifespan, however, the degree of decrease depended on some extent upon the age of the specimens since the previous conjugation. Further, the pulsation rate of the contractile vacuole became lower at this high concentration. 98% of heavy water caused an irreversible injury resulting in immediate death, although some specimens could withstand such a concentration for a few hours.

Tittler (1938) studied the effect of electric current on *E. mobilis*. He reported the following main results: (i) Under the influence of induction current most of the specimens moved abnormally, and were drawn towards the cathode of the break shocks. Disruption and disintegration of the cell occurred, usually at the posterior region. (ii) Injured pieces retained their original polarity and moved in essentially the same manner as the entire cell. (iii) Within 3–8 h after injury, each fragment had regenerated its missing structures, and at the end of 34 h most of the regenerated specimens divided. (iv) Regeneration was accompanied by profound protoplasmic reorganisation changes comparable to those occurring at the time of division. Cortical granules were withdrawn, and new sets developed in the reformed individuals. The macronuclei fused into a relatively small division nucleus followed by the rapid constriction of the latter into eight nodules characteristic of normal specimens. The micronuclei divided mitotically. (v) The presence of both macronuclear and micronuclear material was necessary for complete functional regeneration.

Occurrence and ecology: *Engelmanniella mobilis* is a common limno-terrestrial species present in all biogeographic regions, except Neotropis and Archinotis (e.g., Engelmann 1862, Calkins 1929, Foissner 1994, 1994c, 1998, 1999). It has a low degree of soil autochthonism, but is characteristic for mull and mor soils (Foissner 1987a, p. 123; 1999a, p. 104; Cowling 1994, p. 25). The original type locality of *E. mobilis* is a brook (Boticzbach) near the city of Prague, Czech Republic (Engelmann 1862; new type locality, see next paragraph). The type locality of the synonym *U. halseyi* is a pond in Westchester County (south-east the U.S. state of New York) where, inter alia, *Sphagnum* and *Myriophyllum* were abundant; in the collecting jar *U. halseyi* was present in great abundance (Calkins 1929, p. 59). The sample was collected by H.R. Halsey in 1928. In 1938, Halsey provided Tittler (1938), who made experiments with electric current (see chapter physiology), with an "*U. mobilis*" population. Calkins (1919a, p. 293) found the New York variety (= *U. mobilis americanus*) in October, 1917 in considerable number in an old hay infusion that had been standing for several months in the zoological laboratory of Columbia University in New York. Unfortunately, Calkins (1919a) did not mention where the hay and/or water of the hay infusion was collected, that is, the original type locality of the New York variety is not known, as admitted by Calkins himself (Calkins 1929, p. 59; ICZN 1999, Article 76.1.1).

Foissner (1982) collected the neotype population of *E. mobilis* from the upper soil layer (0–10 cm) of a young, aperiodic flooded fertile plain (local name "Vogelsang") grown with willow-trees near the village of Grafenwörth (48°24'N 15°47'E; Lower Austria) in 1980; due to fixation of this population as neotype, this is now the type locality of *E. mobilis* (ICZN 1999, Article 76.3). The soil populations used by Wirnsberger-Aescht et al. (1990) for the estimation of the morphological variability are from the following localities: (i) Beech forest (0–2 cm; *Fagus*, *Pinus*, *Betula*, *Quercus*) near the village of Baumgarten, Lower Austria (Bn in Table 28; details see "Profil 7" in Foissner et al. 1985, p. 89). Cultured for about three years and used for the electron microscopy of interphasic cells and cysts (Wirnsberger-Aescht et al.

1989, 1990; for details on sample site and autecology of Austrian populations, see below and Foissner et al. 1985). (ii) Soil from rice field near Kumamoto, Japan, collected in February 1988. (iii) Rhizosphere of marsh plants in Anatolia, Turkey, collected in 1988.

The population used for molecular analyses (see above; at least that resulting in AF164134) was isolated from rhizosphere soil from marsh plants in Anatolia, Turkey (Foissner et al. 2004, p. 267). Further records of *E. mobilis* substantiated by morphological data: clear water (Vieusseux, Bessinge) in the surroundings of Geneva, Switzerland (Roux 1901; see also Forel 1904, p. 131 and André 1912, p. 130); soil in USSR (Nikoljuk & Geltzer 1972); soil and moss infusions from Rwanda (Dragesco 2003).

Limnetic and terrestrial records of *E. mobilis* not substantiated by morphological data: typical mull from a floodplain soil with a *Pruno-Fraxinetum* forest in eastern Austria (Foissner et al. 2005, p. 627); lake (Lansersee) in Tyrol, Austria (Dalla Torre 1891, p. 206); various sites (e.g., ditch, *Phragmites* stalk from mouth of the River Schussen) at Lake Constance (Wetzel 1928a, p. 242, 247); very rare in an oxbow lake in Breisgau, Germany (Henderson 1905, p. 19); oxygenic surface layer of ponds in the suburbs of the city of Leipzig, Germany (Wetzel 1928b, p. 314); common on sandy, debris-rich sediments with mass occurrence in winter and spring in the Hamburg Harbour, Germany (Bartsch & Hartwig 1984, p. 557); soil from the city of Memmingen, Germany (Hartmann 1956, p. 194); in the very light grey brown soil, friable, with roots from the Allindelille forest, on the edge of a natural glade, immediately south of the University huts, Denmark (Stout 1968, p. 394); acid mull site (Oaken Grove) and calcareous mull site (Hobbs Hill) in Chiltern Hills, England (Stout 1962, p. 285); few to several specimens in a pond in Lawnhurst, Didsbury, England (Dixon 1920, p. 34); soil samples from the experimental site at the Macaulay Land Use Research Institute's Sourhope Research Station, near Kelso in Southern Scotland (Finlay et al. 2001, p. 363; Esteban et al. 2006, p. 142); in soil samples, including those of wheat field from the vicinity of Pápa (near Szeged?), Hungary (Biczók 1955, Table IV; 1956, p. 139; recorded both *U. mobilis* and *U. halseyi*); moss from sodium-bicarbonate containing soil from near the city of Szeged, Hungary (Biczók 1959, p. 103); solonetz soils in the Hortobágy National park, Hungary (Szabo 1993; 1995, p. 16; 1999, p. 249); shore of Tihany peninsula, Lake Balaton, Hungary (Gellért & Tamás 1958, p. 234); in September in Lake Garda, Italy (Cattaneo 1888, p. 97; 1889, p. 117); alphamesosaprobic area of Canale Maggiore in Lorno-Colorno, Northern Italy (Madoni & Ghetti 1977, p. 42; Madoni 1980, p. 51); during summer in a beta- to alphamesosaprobic experimental stream in Italy (Madoni & Ghetti 1980, p. 277); in March in a draw-well in Italy (Grispini 1938, p. 152); soil from brushwood, in Italy (Luzzatti 1938, p. 101); soil near Pisa, Italy (Brunetti & Carletti 1932, p. 325; for checklist of Italian ciliates, see Dini et al. 1995, p. 70); with a constancy of about 4% in agricultural soils in Slovakia (Tirjaková 1988, p. 499); Turiec River in Slovakia (Tirjaková 1993, p. 135); Slovakia (Matis et al. 1996, p. 10; Tirjaková 2005, p. 21); Lake Geneva, Switzerland (Roux 1900,

p. 464; André 1916, p. 622); infrequent during March in bogs and ponds near Chaux-de-Fonds, Switzerland (Bourqin-Lindt 1919, p. 74); in December more than 100 ind. l^{-1} in a limnetic habitat in Basel, Switzerland (Riggenbach 1922, p. 53); in May in a fish pond in Poland (Czapik 1959, p. 190); excavations (ponds?) near the village of Tschelopetsch and limnetic habitats near Sofia, Bulgaria (Detschewa 1978, p. 78; Detcheva 1992, p. 98); common in sludge cultures from limnetic habitats of the Danube Delta, Romania (Spandl 1926, p. 535); benthos of Volga River (Sassuchin 1924, p. 51; Mamaeva 1979a, p. 409; 1979b, p. 71); various soils from Kangerdlugssuak and from Scoresby Land, East Greenland (Dixon 1939, p. 166; Stout 1970, p. 20); soil in Svalbard (Grandori & Grandori 1934, p. 284); Oka River, Russia (Neiswestnowa-Shadina 1935, p. 573); Russian soils (Dixon 1937, p. 447); soil from the USSR, inter alia, treated with the herbicide Monuron (Gel'cer & Geptner 1976, p. 177); chernozem-meadow soil in Baraba forest, Russia? (Mordkovitch 1977, p. 76); various soils, inter alia, treated with organic manure, from Baruipur, District 24-Parganas and Calcutta, India (Bhat'acharya & Das 1977; Bhattacharya et al. 1977, p. 73); soil from Coimbatore?, South India (Grandori & Grandori 1934, p. 284); soil or lake from the Mount Fuji area, Japan (Sudzuki 1971, p. 194; 1971a, p. 778; 1978, p. 90?); in six of 17 paddy field samples in Japan (Takahashi & Suhama 1991, p. 106); during summer in Reelfoot lake, Tennessee, USA (Bevel 1938, p. 145); from aquaria (inter alia, on sulphur patches) filled with bottom soil from an estuary, in use at the Naragansett Marine Laboratory, Rhode Island, USA (Lackey 1961, p. 277); Cape Fear River in the vicinity of Fayetteville, North Carolina, USA (Cairns & Yongue 1973, p. 32); euphotic portion of water column of the oligotrophic Lake George (Adirondack Park), North-Eastern New York, USA (Richards et al. 2005, p. 1416; identified via rRNA); marshy area near Sheldrick waterfalls, Shimba Hills Nature Reserve, Kenya (Foissner 1999, p. 322); brackish (K_{25} = 4.5 to 12.9 µS cm^{-1}) volcanic crater-lake (Tower Hill) in Victoria, Australia (Finlay et al. 1999, p. 140; Esteban et al. 2000, p. 163); in various New Zealand soils including tussock-grassland soils, inter alia, irrigated with water or sewage effluent (Stout 1958, p. 977; 1960, p. 240; 1978, p. 14); limnetic habitats near Rio de Janeiro, Brazil (Cunha 1913, p. 107). Foissner (1983b) made a recovery experiment and found about 80% of the specimens added, probably because *E. mobilis* is rather large and mobile. Not recorded during detailed surveys of Australian and Namibian soils (Blatterer & Foissner 1988, Foissner et al. 2002a).

Limnetic and terrestrial records of the synonym *U. mobilis americanus* not substantiated by morphological data: limnetic habitats near Barcelona, Spain (Margalef López 1945, p. 376; specimens resembling this variety); soil samples, inter alia, from the Sofia region, Bulgaria (Decheva 1966, p. 145; Detcheva 1972, p. 280; 1992, p. 97); prairie soil from the Lincoln Township area, Polk County, Iowa, USA (Mote 1954, p. 588; Fig. 86s).

Limnetic and terrestrial records of the synonym *U. halseyi* not substantiated by morphological data: soil in Belgium (Chardez 1967, p. 294); benthic in a depth of 12 m in Esthwaite, a eutrophic lake in the English Lake District, UK (Webb 1961, p.

141); rhizosphere of the field of Pápakovácsi, near Szeged(?), Hungary (Biczók 1955, Table IV, p. 31; 1956, p. 139; together with the synonym *U. mobilis*); common and dominant in solonetz soils in the Hortobágy National park, Hungary (Szabo 1986, p. 304; 1986a, p. 273; 1993; 1995, p. 16; 1999, p. 249); very frequent in chernozem soils of the Great Hungarian Plain (Szabo 2000, p. 14); limnetic and terrestrial in various sites (e.g., Black Sea area, Rila Mountain) in Bulgaria (Detcheva 1972, p. 280; 1992, p. 98; Detschewa 1972, p. 77; Decheva 1965, p. 205; 1968, p. 168; 1970, p. 59; 1973, p. 145); Lake Detelinata (Rila Mountains) and Lake Dolno Kremensko (Pirin Mountains), Bulgaria (Detschewa 1978, p. 78); freshwater habitats in Thailand (Charubhun & Charubhun 2000, p. 491); prairie soil from the Lincoln Township area, Polk County, Iowa, USA (Mote 1954, p. 588; Fig. 86t).

Wirnsberger-Aescht et al. (1990) cultivated the Turkish and Japanese population of *E. mobilis* at room temperature in Petri dishes containing salad medium and Eau de Volvic (1:1) and a few wheat grains to stimulate growth of bacteria; the medium was changed about every two weeks. According to Calkins (1929, p. 65), the synonym *U. halseyi* was not as satisfactory for isolation cultures as *U. mobilis americanus* (= New York variety), but it grew well in mass cultures having a pH 7.2–7.4.

Calkins (1919a) used various media to cultivate *E. mobilis*, but the best result was obtained with the following medium: boil 100 mg of chopped hay with 130 mg of flour in 100 ml of spring water for 10 min; dilute this, when 24 h old, with an equal part of fresh spring water. With this medium made fresh every day, the cells divided 1–3 times per day. Gregory (1925) found that young and old specimens are immediately depressed in beef medium, but recover their vitality and may show a greater division rate than that of the control series when transferred to the normal hay-flour medium. Treatment with yeast extract lowered the division rate of *E. mobilis* (Gregory 1928).

Feeds likely on bacteria (Foissner 1982) or diatoms (Gellért & Tamás 1958, p. 234); the synonym *Uroleptus halseyi* feeds on bacteria and detritus according to Szabo (2000, p. 14). Biomass of 10^6 individuals about 34 mg (Foissner 1987a, p. 123; 1998, p. 202). Division rate up to 1.7–3.0 per day (Calkins 1919a; 1919b, p. 128; see also Zaika 1970). Darbyshire et al. (1989) found that the motility, growth rate, predation, and nitrogen excretion considerably declined as soil temperature fell from 20 °C to 2 °C.

Slender forms from mosses

***Uroleptus* spec.** – Kahl, 1932, Tierwelt Dtl., 25: 548, Fig. 92_3 (Fig. 95a). Remarks: Kahl (1932) found several worm-like *Uroleptus*-like forms. The specimen illustrated in Fig. 95a has very prominent (strong) cortical granules ("Protrichocysten") along the marginal rows (against in many longitudinal rows in *E. mobilis*). Nuclear apparatus composed of about 15 linearly arranged macronuclear nodules and at least one micronucleus. Body size not mentioned. Distal end of adoral zone obviously far ex-

tending posteriorly. Contractile vacuole distinctly ahead of mid-body. Movement winding. No further details described. Cirral pattern likely incompletely illustrated. Moss from California, USA.

***Uroleptus* (?) spec.** – Kahl, 1932, Tierwelt Dtl., 25: 548, Fig. 110_{21} (Fig. 77d in Berger 2008, p. 395). Remarks: Body length 200 µm. Body very slender (length:width ratio of specimen illustrated about 22 to 1) and delicate and thus very difficult to observe. Many macronuclear nodules dispersed throughout the cell. Adoral zone occupies only about 8% of body length. Two marginal rows; cirral pattern likely not exactly recognised. Dorsal bristles obviously short (about 3–5 µm). Moss (terrestrial? limnetic?); sample site (Germany? USA?) not mentioned. For brief note, see also Berger (2008, p. 395). Perhaps a *Hemisincirra* (e.g., *H. rariseta*-like; Berger 2008, p. 428) or *Circinella* species (p. 309).

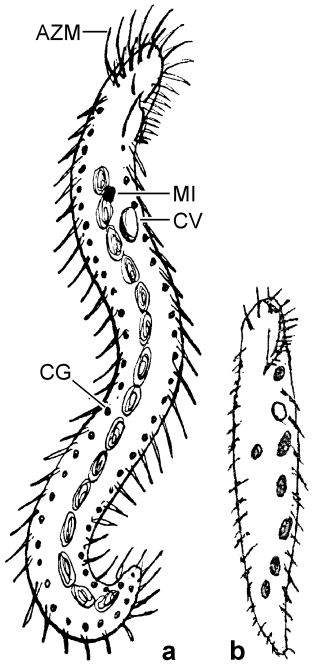


Fig. 95a *Uroleptus* spec. (from Kahl 1932. From life). Ventral view of a specimen from a Californian moss, size not indicated. AZM = adoral zone of membranelles, CG = cortical granules, CV = contractile vacuole, MI = micronucleus. Page 544.

Fig. 95b *Uroleptus mobilis*, insufficient redescription (from Chaudhuri 1929. From life?). Ventral view, about 90 µm. Page 545.

Insufficient redescription

Uroleptus mobilis – Chaudhuri, 1929, Annls Protist., 2: 54, Plate II, 26 (Fig. 95b). Remarks: Chaudhuri (1929) provided a rather simple illustration, but no description. The specimen only agrees in the number of macronuclear nodules (about seven) with relevant descriptions (Engelmann 1862, Foissner 1982), but not in body size (around 90 µm) and shape (too wide). Soil in India (see also Bhatia 1936, p. 369).

Taxa not Considered in the Kahliellidae and its Synonym Parakahliellidae

The following genera and species, included in the kahliellids and parakahliellids by some workers (Tables 5–13), have features clearly indicating that they belong to other higher taxa, for example, the oxytrichids (Berger 1999), the urostyloids (Berger 2006a), the amphisiellids (Berger 2008). Therefore they are not treated in the Kahliellidae. Eigner (1997, 1999) assigned many species, inter alia, several stylonychines, to the Parakahliellidae. However, it is quite evident that the species included do not form a monophyletic group, indicating that the feature neokinetal 1

anlagen development (see Kahliellidae) is not usable, at least not at this level. Eigner (1997) did not include whole genera in the Parakahliellidae, but only species for which details about the cell division are known.

***Amphisiellides illuvialis* Eigner & Foissner, 1994**, J. Euk. Microbiol., 41: 244. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). Now classified in *Nudiamphisiella* Foissner, Agatha & Berger, 2002 because of significant differences to the type species *Amphisiellides atypicus* (Hemberger, 1985) Foissner, 1988 (for details, see Berger 2008, p. 569, 651). The ventral and dorsal infraciliature of *Nudiamphisiella illuvialis* is indeed similar to that of some "parakahliellids", but it has a continuous frontoventral row composed of two parts. This is reminiscent of the amphisiellids, which lack a dorsomarginal kinety (vs. present in *Nudiamphisiella*). Thus, Berger (2008, p. 560) preliminary classified *Nudiamphisiella* as non-oxytrichid Dorsomarginalia. Further studies are needed to find the true phylogenetic position of this species.

***Banyulsella* Dragesco, 1953**, Vie Milieu, 4: 637. Type species (by monotypy): *Banyulsella viridis* Dragesco, 1953. Remarks: First mentioned, but not described (thus a nomen nudum) in a species list by Dragesco (1953a, p. 629). Described in detail by Dragesco (1960, p. 316). Classified in the Kahliellidae by Lynn (2008, p. 357, incertae sedis). The single species, *Banyulsella viridis*, is very small (about 50 µm), has a very large (more than 50% of body length), U-shaped adoral zone, three enlarged frontal cirri, two short and two long "fronto-ventral" cirral rows, and a long row of transverse(?) cirri. Marginal cirri obviously lacking (which would be an apomorphy). One row of fine cirri on rear portion of dorsal side. Six small macronuclear nodules. Mesopsammon of Banyuls-sur-Mer, Mediterranean Sea, France. The habitus is not reminiscent of a kahliellid. Thus, it is not treated in the present book. Jankowski (1975, p. 27) established the Banyulsellidae (incorrectly spelled Banylsellidae) for this species, which will be treated in a later volume of the monograph of hypotrichs.

***Cladotricha* Gaievskaïa, 1925**, Russk. Arkh. Protist., 4: 259, 281. Type species (by original designation): *Cladotricha koltzowii* Gaievskaïa, 1925. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115), Tuffrau & Fleury (1994, p. 137), Lynn & Small (2002, p. 456), Jankowski (2007, p. 461), and Lynn (2008, p. 357). I preliminary classify it in the Gonostomatidae (p. 235).

***Clara pustulata* (Müller, 1786) Eigner, 1997**, Animalcula Infusoria, p. 246. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). Type of *Clara* Eigner, 1997 and *Tetmemena* Eigner, 1999. Now *Tetmemena pustulata* (Müller, 1786) Eigner, 1999 because *Clara* Eigner, 1997 is a junior homonym. Typical stylonychine because of the oxytrichid dorsal kinety fragmentation, the rigid body, and the lack of cortical granules (for review, see Berger 1999, p. 565, 591, not yet classified in *Tetmemena*). The position in the Stylonychinae is also supported by molecular data (e.g., Sonntag et al. 2008).

***Clara vorax* (Stokes, 1885) Eigner, 1997**, Am. mon. micros. J., 6: 188. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). Now *Tetmemena vorax* (Stokes, 1885) Eigner, 1999. A typical stylonychine oxytrichid according to morphological data (for review, see Berger 1999, p. 591).

***Coniculostomum* Njine, 1979**, Protistologica, 15: 353. Type species (by monotypy): *Laurentia monilata* Dragesco & Njine, 1971. Remarks: Classified in the Kahliellidae by Eigner (1995, p. 363) and in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). However, relevant morphological data strongly indicate that *Coniculostomum* is the sistergroup of *Stylonychia* Ehrenberg, 1830 (Berger & Foissner 1997; Berger 1999, p. 606).

***Cyrtohymena muscorum* (Kahl, 1932) Foissner, 1989**, Tierwelt Dtl., 25: 613. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). Type species of *Cyrtohymena* Foissner, 1989. It certainly belongs to the oxytrichids as clearly indicated by the presence of an oxytrichid dorsal kinety 3 fragmentation (Berger & Foissner 1997). The presence of cortical granules, the very flexible body, the "short" (≤35% of body length) adoral zone, and the participation of the postoral ventral cirrus V/3 in primordia formation show that it is a non-stylonychine oxytrichid (for review, see Berger 1999, p. 281; Voss 1991). This is supported by the phylogenetic position of the morphologically very similar *Cyrtohymena citrina*, which clusters close to *Paraurostyla weissei* (see below) in molecular trees (e.g., Foissner et al. 2004, Sonntag et al. 2008, Paiva et al. 2009). By contrast, some other "*Cyrtohymena*" species have a more or less rigid body and a rather large adoral zone and lack cortical granules. In addition, the arrangement of the postoral ventral cirri is different. Berger (1999, p. 280, 314, 317, 320) already supposed that in these species the rearmost postoral ventral cirrus (V/3) is not involved in primordia formation, indicating that they likely belong to the stylonychines. Song (2004a) studied the cell division in *Cyrtohymena tetracirrata* (Gellért, 1942) Foissner, 1989. His Figures 1F, 2C, E, G clearly show that cirrus V/3 does not participate in primordia formation. Thus, I assume that Song (2004a) overlooked this cirrus in some early dividers (his Fig. 1E, 2A).[1] The photomicrographs in Song (2004a) are rather dark. In his Figure 11, which shows a middle divider, he marked only the two less important pretransverse ventral cirri, but somewhat ahead of the upper arrowhead the parental cirrus V/3 is recognisable. Thus, the differences mentioned above demand the removal of the "rigid *Cyrtohymena* species" from *Cyrtohymena* and the establishment of a new genus in the Stylonychinae. Thus, I establish the genus *Rigidohymena* gen. nov: Stylonychinae (rigid body, cortical granules lacking, adoral zone 40% or more of body length, postoral ventral cirrus V/3 not involved in primordia formation) with

[1] Song (2004a, p. 252) wrote "Three postoral ventral and 2–3 posterior frontal cirri *appear* to contribute to the formation of these anlagen." The word appear demonstrates that he was uncertain and, in addition, in the discussion he did not mention this important feature of the stylonychines (Berger 1997, Berger 1999).

Cyrtohymena-like oral apparatus and (more or less) 18 frontal-ventral-transverse cirri. One left and one right marginal row. Caudal cirri present. *Oxytricha*-like dorsal kinety pattern, that is, dorsomarginal kinety(ies) and fragmentation of kinety 3 present.

Type species: *Steinia tetracirrata* Gellért, 1942.

Etymology: *Rigidohymena* is a composite of the Latin adjective *rigidus* (rigid, inflexible) and the second part of the genus-group name *Cyrtohymena* (Greek noun *ho hymen*; cuticle, thin skin, membrane); it shall simply indicate that the species included have a rigid body and were previously classified in *Cyrtohymena*. *Rigidohymena* is, like *Cyrtohymena*, of feminine gender (Aescht 2001, p. 280).

Species assignable: *Rigidohymena tetracirrata* (Gellért, 1942) comb. nov. (basionym *Steinia tetracirrata* Gellért, 1942); *Rigidohymena quadrinucleata* (Dragesco & Njine, 1971) comb. nov. (basionym *Steinia quadrinucleata* Dragesco & Njine, 1971); *Rigidohymena inquieta* (Stokes, 1887) comb. nov. (basionym *Histrio inquietus* Stokes, 1887); *Rigidohymena candens* (Kahl, 1932) comb. nov. (basionym *Oxytricha (Steinia) candens* Kahl, 1932).

Remarks: Although the separation is not yet confirmed by molecular data, I am sure that it is a small, but meaningful step to unravel the systematics of the hypotrichs, inasmuch as the Stylonychinae with the features mentioned above are the sole group which is stable within all molecular trees. The permanent validation of this morphologically well defined group by molecular methods strongly indicates (actually proves) that the defining features are correctly selected. The remaining "true" *Cyrtohymena* species belong either to *Cyrtohymena (Cyrtohymena)* Foissner, 1987 or *Cyrtohymena (Cyrtohymenides)* Foissner, 2004. Due to the possession of dorsomarginal kineties and a fragmentation of kinety 3 *Cyrtohymena* belongs to the non-stylonychine part of the oxytrichids (Berger 2008). Of course this splitting requires the assumption that the characteristic "cyrtohymenid" undulating membrane pattern evolved two times independently, except we suppose that *Cyrtohymena* and the stylonychines had the same last common ancestor which already had a cyrtohymenid oral apparatus.

Deviata **Eigner, 1995**, Europ. J. Protistol., 31: 343. Type species (by original designation): *Deviata abbrevescens* Eigner, 1995. Remarks: Classified in the Kahliellidae by Eigner (1995), Jankowski (2007, p. 461), and Lynn (2008, p. 357). Assigned to the Oxytrichidae by Eigner (1997, p. 555) and not considered by Eigner (1999, p. 46). I treat it as taxon of unknown position in the non-dorsomarginalian hypotrichs (p. 555).

Epiclintes **Stein, 1863**, Amtliche Berichte Deutscher Naturforscher und Aerzte in Karlsbad, 37: 162. Type species (by subsequent designation by Stein 1864, p. 44): *Oxytricha auricularis* Claparède & Lachmann, 1858. Remarks: Classified in the Kahliellidae by Song & Wang (1999, p. 73). An urostyloid reviewed by Berger (2006a, p. 1116). Recently, Hu et al. (2009a) described a new subspecies.

***Eschaneustyla* Stokes, 1886**, Proc. Am. phil. Soc., 23: 28. Type species (by original designation): *Eschaneustyla brachytona* Stokes, 1886. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115). However, *Eschaneustyla* very likely belongs to the urostyloids, although the midventral cirral pattern is not clearly recognisable (for review, see Berger 2006a, p. 1146).

***Gastrostyla steinii* Engelmann, 1862**, Z. wiss. Zool., 11: 383. Remarks: Type of *Gastrostyla* Engelmann, 1862. Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). Classified in the oxytrichids by Berger (1999, p. 791) because of the dorsal kinety fragmentation, a hypothesis later supported by molecular data (Foissner et al. 2004). The rigid body and the lack of cortical granules support the molecular placement in the stylonychines. See Berger (2008, p. 138f) for further details.

***Hemicycliostyla* Stokes, 1886**, Proc. Am. phil. Soc., 23: 22. Type species (by subsequent designation by Jankowski 1979, p. 55): *Hemicycliostyla sphagni* Stokes, 1886. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115) and Tuffrau & Fleury (1994, p. 137). Very likely a urostyloid (for review, see Berger 2006a, p. 811).

***Histriculus muscorum* (Kahl, 1932) Corliss, 1960**, Tierwelt Dtl., 25: 617. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). Now *Sterkiella histriomuscorum* (Foissner et al., 1991) Foissner et al., 1991, a stylonychine oxytrichid according to morphological, morphogenetic, and molecular data (e.g., Berger 1999, p. 683; Foissner et al. 2004, Sonntag et al. 2008).

***Kerona polyporum* Ehrenberg, 1835**, Abh. preuss. Akad. Wiss., 1835: 164. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). Synonym of the type species *K. pediculus* (Müller, 1773) Blochmann, 1886, an oxytrichid reviewed by Berger (1999, p. 826). This species has dorsomarginal kineties, a very complex multiple fragmentation, a long adoral zone, lacks cortical granules, and has a rather firm body indicating that it is a member of the stylonychines (Berger 1999). However, this presumed position has to be checked by meaningful molecular data.

***Lacazea* Dragesco, 1960**, Trav. Stn biol. Roscoff, 12: 330. Type species (by original designation): *Lacazea ovalis* Dragesco, 1960. Remarks: Classified in the Kahliellidae by Lynn (2008, p. 358, incertae sedis). *Lacazea ovalis* is almost circular in outline, has a single macronucleus (indicating that it is a euplotid), and a difficult-to-interpret cirral pattern, which is not reminiscent of a kahliellid. *Lacazea* will be reviewed in a later volume of the monograph of hypotrichs.

***Laurentia acuminata* Fedriani, Martin & Pérez-Silva, 1976**, Boln R. Soc. esp. Hist. nat., 74: 67. Remarks: *Laurentiella acuminata* (Fedriani et al., 1976) Martin et

al., 1983 is classified in the Kahliellidae by Eigner (1995, p. 363). I is a junior synonym of *Laurentiella strenua* (Dingfelder, 1962) Berger & Foissner, 1989, which I assigned to the Stylonychinae because of the complex dorsal ciliature, the rigid body, and the *Stylonychia*-like oral apparatus (Berger 1999, p. 753). So far, this position is not yet supported by molecular data. However, a position outside the stylonychines would be a great surprise.

Notohymena rubescens **Blatterer & Foissner, 1988**, Stapfia, 17: 71. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). This species, which is the type of *Notohymena* Blatterer & Foissner, 1988, shows the typical oxytrichid fragmentation of dorsal kinety 3. The presence of cortical granules and the flexible body indicate that it is a non-stylonychine oxytrichid. For review, see Berger (1999, p. 324).

Onychodromus grandis **Stein, 1859**, Lotos, 9: 4. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). A typical stylonychine hypotrich according to morphological data (for review, see Berger 1999, p. 724), a classification supported by molecular data (e.g., Sonntag et al. 2008).

Onychodromus quadricornutus **Foissner, Schlegel & Prescott, 1987**, J. Protozool., 32: 144. Remarks: Classified in the Kahliellidae by Eigner (1995, p. 363) and in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). Because of the complex dorsal ciliature (dorsomarginal kineties and multiple fragmentation present) and the rigid body I assigned this species to the Stylonychinae (Berger 1999, p. 738), a position later supported by molecular data (e.g., Bernhard et al. 2001, Li & Song 2006). Later, we established *Styxophrya* Foissner et al., 2004 for this species (*Styxophrya quadricornuta*).

Paragastrostyla **Hemberger, 1985**, Arch. Protistenk., 130: 407. Type species (by original designation): *Paragastrostyla lanceolata* Hemberger, 1985. Remarks: Classified in the Kahliellidae by Tuffrau (1987, p. 115). *Paragastrostyla* has midventral cirri and is therefore classified in the urostyloids (for review, see Berger 2006a, p. 613).

Paraholosticha **Kahl, 1932**, Tierwelt Dtl., 25: 545. Remarks: Kahl (1932) did not fix a type species; thus, the genus is invalid (ICZN 1999, Article 13.3). Replaced by *Paraholosticha* Wenzel, 1953 (Arch. Protistenk., 99: 104; type by original designation: *Paraholosticha muscicola* Kahl, 1932). Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115). *Paraholosticha* and the adelphotaxon *Keronopsis* Penard, 1922 have two highly interesting features, namely, (i) many frontal cirri forming a single corona, and (ii) the division is done in cysts (e.g., Berger & Foissner 1987, Dieckmann 1988, 1989). These features indicate that the *Paraholosticha* + *Keronopsis* group does not belong to the Kahliellidae. Consequently, it will be treated in one of the next volumes of the monograph of the Hypotricha.

***Paraurostyla* Borror, 1972**, J. Protozool., 19: 9. Type species (by original designation): *Urostyla weissei* Stein, 1859. Remarks: *Paraurostyla*, respectively the type species *P. weissei* was classified in the Kahliellidae by Eigner (1995, p. 363) and Lynn & Small (2002, p. 456), and in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). *Paraurostyla* species have several cirral rows covering the ventral side. For that reason *Paraurostyla* was assigned to the kahliellids. Other workers classified it in the oxytrichids because the formation of the ventral and dorsal infraciliature strongly indicates a close relationship with the 18-cirri oxytrichids (e.g., Borror 1979, Wirnsberger et al. 1985). The complex dorsal ciliature (fragmentation of kinety 3, dorsomarginal rows), the flexible body, and the cortical granules indicate that it belongs to the non-stylonychine oxytrichids (for review, see Berger 1999, p. 841). Later, this relationship was supported by molecular data (e.g., Bernhard et al. 2001, Hewitt et al. 2003). More recent data indicate a close relationship with the flexible *Cyrtohymena* species and *Neokeronopsis* (Foissner & Stoeck 2008; see also Berger 2006a, p. 1190).

***Parentocirrus* Voß, 1997**, Europ. J. Protistol., 33: 31. Type species (by original designation): *Parentocirrus hortualis* Voß, 1997. Remarks: Classified in the Kahliellidae by Voß (1997) and Lynn & Small (2002, p. 456) and in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). I assigned *Parentocirrus* to the oxytrichids because of the complex dorsal ciliature (fragmentation of kinety 3 and dorsomarginal rows present; for review see Berger 1999, p. 878). For a detailed description, including morphogenesis and physiological reorganisation, of two Austrian populations of *P. hortualis*, see Blatterer & Foissner (2003). *Parentocirrus hortuliseri* in Lynn & Small (2002, p. 457) is an incorrect subsequent spelling.

***Pattersoniella vitiphila* Foissner, 1987**, Zool. Beitr., 31: 207. Remarks: Type of *Pattersoniella* Foissner, 1987. Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). The dorsal kinety fragmentation, the rigid body, the lack of cortical granules, and the long adoral zone unequivocally assign this species to the Stylonychinae (for review, see Berger 1999, p. 766). This classification was later supported by molecular data (e.g., Bernhard et al. 2001, Sonntag et al. 2008).

***Periholosticha* Hemberger, 1985**, Arch. Protistenk., 130: 403. Type species (by original designation): *Periholosticha lanceolata* Hemberger, 1985. Remarks: Classified in the Kahliellidae by Tuffrau (1987, p. 115). *Periholosticha* has an admittedly inconspicuous midventral pattern and is thus classified in the urostyloids (for review, see Berger 2006a, p. 498).

***Pseudokahliella* Berger, Foissner & Adam, 1985**, Protistologica, 21: 309. Type species (by original designation): *Kahliella marina* Foissner, Adam & Foissner, 1982. Remarks: Originally and later classified in the Kahliellidae (Berger et al. 1985, Tuffrau 1987, Tuffrau & Fleury 1994, Lynn & Small 2002, Jankowski 2007, Lynn 2008). Now listed as incertae sedis in the non-dorsomarginalian hypotrichs (p. 551).

***Pseudouroleptus* Hemberger, 1985**, Arch. Protistenk., 130: 398. Type species (by original designation): *Pseudouroleptus caudatus* Hemberger, 1985. Remarks: Classified in the Kahliellidae by Tuffrau (1987, p. 115) and Lynn (2008, p. 358; as incertae sedis). The type species shows a dorsal kinety fragmentation and therefore this species was classified in the oxytrichids (for review, see Berger 1999, p. 888). For a redescription of the type species and the description of the subspecies *P. caudatus namibiensis*, see Foissner et al. (2002) and the review by Berger (2008, p. 658). "*Pseudouroleptus*" species which lack a dorsal kinety fragmentation are now assigned to *Bistichella* Berger, 2008 (p. 532) and *Metauroleptus* Foissner et al., 2008a.

***Psilotricha* Stein, 1859**, Lotos, 9: 5. Type species (by original designation): *Psilotricha acuminata* Stein, 1859. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115). *Psilotricha* has only few cirri strongly indicating that it does not belong to the kahliellids, which usually have distinct cirral rows. Likely it belongs to the Oxytrichidae (Esteban et al. 2001). However, it is not included in the relevant monograph (Berger 1999, p. 894) because I did not recognise this relationship from Stein's (1859, 1959a) description. It will be reviewed in one of the next volumes of the hypotrich monograph. In my monograph (Berger 1999, p. 894) I incorrectly wrote that *P. acuminata* is described in detail by Stein (1859) and Foissner (1983). However, Foissner (1983) did not describe *P. acuminata*, but *P. succisa*, which is now classified in *Urospinula* Corliss, 1960 (Esteban et al. 2001).

***Spirofilopsis* Corliss, 1960**, J. Protozool., 7: 276. Type species (by original designation): *Spirofilum tubicola natans* Gelei, 1944. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115). Very likely not a kahliellid and thus not treated in the present monograph.

***Steinia sphagnicola* Foissner, 1989**, Sber. öst. Akad. Wiss., 196: 235. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46). A typical stylonychine oxytrichid according to morphological and morphogenetic data (Berger & Foissner 1997; Berger 1999, p. 632). Later, this classification was corroborated by molecular analyses (e.g., Bernhard et al. 2001, Sonntag et al. 2008).

***Thigmokeronopsis* Wicklow, 1981**, Protistologica, 17: 331, 348. Type species (by original designation): *Thigmokeronopsis jahodai* Wicklow, 1981. Remarks: Classified in the Kahliellidae by Song & Wang (1999, p. 73). *Thigmokeronopsis* belongs to the urostyloids (for review, see Berger 2006a, p. 836).

***Trachelochaeta* Šrámek-Hušek, 1954**, Arch. Protistenk., 100: 265. Type species (by original designation): *Trachelochaeta bryophila* Šrámek-Husek, 1954. Remarks: Classified in the Kahliellidae by Lynn & Small (2002, p. 456) and Lynn (2008, p. 357). I classify this little known taxon as incertae sedis in the Gonostomatidae (p. 300).

***Uncinata* Bullington, 1940**, Pap. Tortugas Lab., 32: 207. Type species (by original designation and monotypy): *Uncinata gigantea* Bullington, 1940. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115). This taxon is only known from the original description. Very likely it belongs to the urostyloids and was therefore reviewed by Berger (2006a, p. 1186).

***Uroleptoides* Wenzel, 1953**, Arch. Protistenk., 99: 107. Type species (by original designation and monotypy): *Uroleptoides kihni* Wenzel, 1953. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115). Very likely an amphisiellid and therefore reviewed by Berger (2008, p. 224).

***Uroleptopsis* Kahl, 1932**, Tierwelt Dtl., 25: 543. Type species (by original designation): *Uroleptopsis citrina* Kahl, 1932. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115). A pseudokeronopsid redescribed and reviewed by Berger (2004; 2006a, p. 980).

***Uroleptus* Ehrenberg, 1831**, Abh. preuss. Akad. Wiss., year 1831: 116. Type species (by subsequent designation by Borror 1972, p. 12): *Trichoda musculus* Müller, 1773. Remarks: For problems with the fixation of the type species, see Foissner et al. (1991), Aescht (2001), and Berger (2001). *Uroleptus* species and species of its supposed synonym *Paruroleptus* have zigzagging cirri and therefore have been assigned to the urostylids/holostichids by most authorities (e.g., Borror 1972, Corliss 1979, Hemberger 1982, Borror & Wicklow 1983, Wiackowski 1988, Foissner & Foissner 1988, Shi et al. 1999, Eigner 2001, Lynn & Small 2002, Lynn 2008). Only Tuffrau (1979, p. 525; 1987, p. 115) and Tuffrau & Fleury (1994) assigned it to the Kahliellidae.

Molecular studies suggested that the inclusion of *Uroleptus* in the urostyloids is incorrect (Hewitt et al. 2003, Croft et al. 2003, Foissner et al. 2004). Thus, we put forward the CEUU hypothesis which tries to explain the convergent evolution of the zigzag pattern of the ventral cirri in *Uroleptus*, the urostyloids, and some other taxa, including oxytrichids (Foissner et al. 2004; see also Berger 2006a).

A very close relationship of *Uroleptus* and the kahliellids is rather unlikely because of the different cirral patterns. However, both belong to the non-oxytrichid Dorsomarginalia, a paraphyletic assemblage. The Uroleptidae and some *Uroleptus*-like hypotrichs will be treated in the next volume of the monograph.

***Urosomoida agiliformis* Foissner, 1982**, Arch. Protistenk., 126: 117. Remarks: Classified in the Parakahliellidae by Eigner (1997, p. 555; 1999, p. 46) and in the oxytrichids by Berger (1999, p. 356). The classification of this species is insecure. Previously, we assigned *Urosomoida* Hemberger in Foissner, 1982 to the oxytrichids because it is basically an 18-cirri hypotrich which has lost few transverse cirri (Berger & Foissner 1997; Berger 1999, p. 345). *Urosomoida* has a dorsomarginal kinety, but lacks the characteristic oxytrichid kinety fragmentation. Earlier, we hypothesised that the fragmentation was lost in *Urosomoida* (Berger & Foissner 1997, Berger 1999), whereas now I prefer the assumption that *Urosomoida* is not an oxytrichid, but a

non-oxytrichid Dorsomarginalia (Berger 2008, p. 46). Note that the 18-cirri pattern is not an apomorphy of the oxytrichids (Berger & Foissner 1997, Berger 1999), but of the Hypotricha (Berger 2007; 2008, p. 23; 2008a).

***Urospinula* Corliss, 1960**, J. Protozool., 7: 276. Type species (by original designation): *Urospina bicaudata* Gelei, 1944. Remarks: Classified in the Kahliellidae by Tuffrau (1979, p. 525; 1987, p. 115). The type species was redescribed in detail by Foissner (1983) as *Psilotricha succisa* (Müller, 1786) Foissner, 1983. At present there is no strong evidence that *Urospinula* belongs to the kahliellids. Thus, it will be reviewed in a later volume.

***Wallackia* Foissner, 1976**, Acta Protozool., 15: 390. Type species (by original designation): *Wallackia schiffmanni* Foissner, 1976. Remarks: Classified in the Kahliellidae by Lynn & Small (2002, p. 456) and Lynn (2008, p. 357). I follow Small & Lynn (1985) and assign it to the Gonostomatidae (Table 3; p. 206).

Taxa of Unknown Position in the Non-dorsomarginalian Hypotricha

The phylogenetic position of the genera *Deviata*, *Orthoamphisiella*, *Pseudokahliella*, *Saudithrix*, and *Stenotricha* is uncertain. All lack dorsomarginal kineties and kinety fragmentation, strongly indicating that they do not belong to the dorsomarginalian branch of the Hypotricha. For more detailed discussion about this topic, see remarks at genus and species sections. In addition, a supplement to *Apourosomoida* – already reviewed in Berger (2008, p. 514) – is provided.

Deviata Eigner, 1995

1995 ***Deviata* nov. gen.**[1] – Eigner, Europ. J. Protistol., 31: 343 (original description). Type species (by original designation): *Deviata abbrevescens* Eigner, 1995.
2001 ***Deviata* Eigner 1995** – Aescht, Denisia, 1: 57 (catalogue of generic names of ciliates).
2001 ***Deviata* Eigner, 1995** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 17 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Deviata* Eigner, 1995**[2] – Lynn & Small, Ciliophora, p. 457 (guide to ciliate genera).
2007 ***Deviata* Eigner, 1995** – Jankowski, Ciliophora, p. 461 (revision of ciliates).
2008 ***Deviata* Eigner, 1995** – Lynn, Ciliated protozoa, p. 357 (revision of ciliates).

Nomenclature: *Deviata* is, according to Eigner (1995), derived from *devius* (Latin; aside its way) because anlagen are generated by deviating multiple within anlagen. Feminine gender (Eigner 1995; Aescht 2001, p. 280).

Characterisation (A = supposed apomorphy): Non-dorsomarginalian hypotrich. Body circular or elliptical in cross section, that is, not distinctly flattened dorsoventrally (A?). Adoral zone of membranelles roughly gonostomatid. Undulating membranes relatively short, almost straight, not intersecting. Three frontal cirri. Usually one buccal cirrus. Two or three long frontoventral rows, leftmost terminating about in mid-body. Pretransverse ventral and transverse cirri lacking. Two or more left marginal rows (A?) and one or more right marginal rows. One, two (type species), or three dorsal kineties. Dorsomarginal kinety, dorsal kinety fragmentation, and caudal cirri lacking. Rightmost frontoventral row originates from a primary primordium. Limnetic and terrestrial.

[1] Eigner (1995) provided the following diagnosis: Kahliellidae with more than one long cirral row on right and left lateral side of body. One of the long cirral rows right of adoral zone of membranelles terminates in center of ventral surface. Typical parental (old) cirral rows absent. Multiple within anlagen develop during morphogenesis.

[2] Lynn & Small (2002) provided the following characterisation: Midventral surface barren; at least one ventral cirral file extending adjacent to left marginal cirral file, which may be on dorsal surface; midventral cirral file obliquely extends into midventral surface and terminates; no parental cirri remain during division morphogenesis; transverse cirri, absent; caudal cirri, absent.

Additional characters: Body flexible, but usually not or only slightly contractile. Macronuclear nodules almost in midline of cell or slightly left of it. Contractile vacuole about in mid-body near left cell margin, except for *D. estevesi* where it is displaced towards midline. Cortical granules lacking. Ordinary cirri usually composed of two or four cilia only. Dorsal bristles 2–4 μm long, except for *D. spirostoma* where they are 8–12 μm long.

Remarks: Eigner (1995) assigned *Deviata* to the Kahliellidae, however, without detailed explanation. Further, he did not compare *Deviata* with "closely related" and similar genera, but he merely made a comparison of *D. abbrevescens* (type species) and *Kahliella bacilliformis*, which he transferred to *Deviata* because they have a very similar cirral pattern (p. 578). Lynn & Small (2002), Küppers et al. (2007, p. 446), Jankowski (2007), and Lynn (2008) took over the original classification of *Deviata* in the Kahliellidae, although Eigner (1997) eliminated this group and classified *Deviata* in the Oxytrichidae, more precisely as "supposed ancestor" of the Oxytrichidae. I am also uncertain about the phylogenetic position of *Deviata*, but according to my current hypothesis it is a non-dorsomarginalian hypotrich because it lacks both the dorsal kinety fragmentation of the oxytrichids and the dorsomarginal row of the Dorsomarginalia (Berger 2006a, 2008). Ontogenetic data of some species show that *Deviata* forms six (I–VI) frontal-ventral cirri anlagen.

A position of *Deviata* in the kahliellids is unlikely because parental cirral rows are not retained after division; in addition, a dorsomarginal kinety, a feature (very likely) present in *Kahliella*, is lacking in *Deviata*. Perhaps it is related to *Orthoamphisiella* because the rightmost frontoventral row originates in a very similar (homologous?) way, namely, via a primary primordium formed about in the mid-portion of the parental row VI (Fig. 96k–m, 105n–q). However, the further development of this row in the proter proceeds in a rather different way in *Orthoamphisiella* and *Deviata* (details see *O. stramenticola* and *D. abbrevescens*). Further, all frontoventral row anlagen of *Orthoamphisiella* originate via primary primordia whereas this mode occurs only in the rightmost anlage in *Deviata*; the remaining anlagen in *Deviata* originate independent from each other in proter and opisthe.

However, not only the rough phylogenetic position of *Deviata* is difficult to estimate, but also the species belonging to this genus. Only for the half of species the cell division is known, and molecular data are lacking for all species. Thus, the assignment of the eight species included is mainly based on similarities in the relatively simple cirral pattern, which, unfortunately, does not show specific features, except for the posteriorly shortened leftmost long frontoventral row. Thus, nonmonophyly of *Deviata* cannot be excluded.

Neogeneia Eigner, 1995 has a rather similar general appearance (p. 481). However, in this genus parental cirri are retained in postdividers. For that reason it is (preliminary) assigned to the kahliellids.

Perisincirra Jankowski, 1978 differs from *Deviata* mainly in the much more widely spaced cirri and the presence of caudal cirri, at least in the two species described by Foissner et al. (2002a; p. 463 of present book).

Species included in *Deviata* (alphabetically arranged basionyms are given): (1) *Deviata abbrevescens* Eigner, 1995 (type species); (2) *Deviata brasiliensis* Siqueira-Castro, Paiva & Silva-Neto, 2009; (3) *Deviata polycirrata* Küppers & Claps, 2010; (4) *Deviata rositae* Küppers, Lopretto & Claps, 2007; (5) *Kahlia bacilliformis* Gelei, 1954; (6) *Kahliella quadrinucleata* Dragesco, 2003; (7) *Kahliella spirostoma* Alekperov, 1988. Incertae sedis: (8) *Deviata estevesi* Paiva & Silva-Neto, 2005.

Key to *Deviata* species

Identification of *Deviata* species is difficult because several of them are very slender and therefore the exact cirral pattern is hardly discernible in life. Furthermore, the cirral pattern is rather similar in all species so that protargol impregnation is almost indispensable, all the more as you also need the number of dorsal kineties and/or the number of adoral membranelles to identify your specimens/population. See also Table 31a for listing of main differences. When you cannot identify your population with the key below, see also *Neogeneia* (p. 481), *Perisincirra* (p. 463), and *Engelmanniella* (p. 498).

1 7–14, usually 8 or 9 macronuclear nodules (Fig. 103a–c). . . . . *Deviata rositae* (p. 606)
- 2–4 macronuclear nodules (e.g., Fig. 96b, 98a–c, 99a, b, 101a, b, 104b, h–j). . . **2**

2 45–50 adoral membranelles; 3 dorsal kineties (Fig. 101a, b, 102a–c). **6**
- 18–33 adoral membranelles; 1 or 2 dorsal kineties (e.g., Fig. 98b, e, f). **3**

3 One dorsal kinety (Fig. 98f). . . . . *Deviata bacilliformis* (p. 578)
- Two dorsal kineties (e.g., Fig. 96h, 99c, 104l). **4**

4 Usually 4 macronuclear nodules (Fig. 99a–c, 100a, b). **7**
- Usually 2 (rarely 4) macronuclear nodules. **5**

5 Body length:width ratio about 9:1 in life, that is, body very slender; contractile vacuole near left cell margin; in total about 7 long cirral rows; 1 short frontal row (= parabuccal row) and usually 1 buccal cirrus; dorsal kinety 2 with very long break (Fig. 96a, b, g, h). . . . . *Deviata abbrevescens* (p. 565)
- Body length:width ratio about 2.5:1 in life, that is, body broad elliptical; contractile vacuole almost in cell midline; in total about 11 long cirral rows; 2 short frontal rows (= parabuccal row and buccal? row); dorsal kinety 2 without break, but dikinetids widely spaced in rear half (Fig. 104a–n). *Deviata estevesi* (p. 609)

6 (2) About 19 cirral rows (Fig. 102a–c). . . . . *Deviata polycirrata* (p. 598)
- About 8 cirral rows (Fig. 101a, b). . . . . *Deviata spirostoma* (p. 597)

7 (4) Dorsal kinety 2 with normally spaced dikinetids, but likely with break about in mid-kinety (Fig. 99c). . . . . *Deviata quadrinucleata* (p. 588)
- Dorsal kinety 2 with very widely spaced dikinetids in middle and posterior portion, anteriorly likely distinctly shortened (Fig. 100b). . . . . *Deviata brasiliensis* (p. 590)

Table 31 Morphometric data on *Deviata abbrevescens* (abb, from Eigner 1995), *Deviata bacilliformis* (ba1, from Berger & Foissner 1987; ba2, population I from Dragesco 2003; ba3, population II from Dragesco 2003; ba4, from Küppers & Claps 2010), *Deviata brasiliensis* (bra, from Siqueira-Castro et al. 2009), *Deviata estevesi* (es1, from Paiva & Silva-Neto 2005; es2, from Siqueira-Castro et al. 2009), *Deviata polycirrata* (pol, from Küppers & Claps 2010), *Deviata quadrinucleata* (qua, from Dragesco 2003), *Deviata rositae* (ros, from Küppers et al. 2007), and *Uroleptus elongatus* (elo, supposed synonym of *D. abbrevescens*; from Fernandez-Leborans 1981) [y]

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	abb	172.4	152.0	54.4	–	31.0	90.0	300.0	25
	ba1	124.1	122.0	7.8	2.0	6.3	112.0	145.0	15
	ba2	132.0	131.0	25.7	4.5	19.0	98.0	173.0	33
	ba3	194.0	200.0	17.2	4.9	9.0	161.0	218.0	13
	ba4 [i]	105.7	105.0	28.5	–	–	65.0	154.0	10
	ba4	111.0	112.0	12.9	–	–	98.0	133.0	15
	bra	107.2	104.0	24.2	–	22.6	62.0	160.0	45
	elo [s]	124.0	–	–	–	–	–	–	?
	es1	86.2	84.0	7.4	1.5	8.6	75.0	100.0	25
	es2	85.3	80.0	17.9	–	20.9	67.0	138.0	25
	pol [i]	152.0	150.0	16.8	–	–	130.0	180.0	10
	pol	181.2	172.5	20.9	–	–	155.0	220.0	20
	qua	97.0	100.0	7.2	1.9	7.4	86.0	106.0	14
	ros [i]	128.3	126.0	12.3	–	–	112.0	154.0	15
	ros	129.5	126.0	13.7	–	–	98.0	154.0	20
Body, width	abb	27.1	28.0	6.8	–	25.1	16.0	40.0	25
	ba1	19.3	19.0	2.0	0.5	10.3	17.0	25.0	15
	ba2	29.0	27.0	6.6	1.2	22.0	18.0	45.0	33
	ba3	32.0	31.0	3.0	0.9	9.0	23.0	36.0	13
	ba4 [i]	44.8	42.0	10.0	–	–	35.0	70.0	10
	ba4	56.5	56.0	8.0	–	–	42.0	70.0	15
	bra	43.9	43.0	8.1	–	18.4	28.0	64.0	45
	elo [s]	17.0	–	–	–	–	–	–	?
	es1	42.7	44.0	8.7	1.8	20.4	27.0	60.0	25
	es2	38.0	36.0	8.5	–	22.5	26.0	60.0	25
	pol [i]	61.5	65.0	10.0	–	–	45.0	70.0	10
	pol	130.2	127.5	21.2	–	–	100.0	180.0	20
	qua	44.0	46.0	7.7	2.1	17.0	30.0	54.0	14
	ros [i]	22.2	21.0	2.5	–	–	21.0	28.0	15
	ros	41.8	42.0	9.2	–	–	24.5	56.0	20
Adoral zone of membranelles, length	abb	27.7	28.0	2.7	–	9.7	23.0	32.0	20
	ba1	23.7	24.0	1.8	0.5	7.8	21.0	27.0	15
	ba2	23.0	23.0	1.2	0.2	5.0	21.0	26.0	33
	ba3	30.0	31.0	2.9	0.8	10.0	27.0	36.0	13
	ba4	24.0	24.5	2.2	–	–	21.0	28.0	15
	bra	20.8	21.0	2.5	–	11.9	14.0	25.0	45
	elo [s]	28.0	–	–	–	–	–	–	?
	es1	32.5	32.5	2.9	0.6	8.8	28.0	40.0	22
	es2	32.5	33.0	2.9	–	8.6	25.0	38.0	24
	pol	54.7	55.0	5.2	–	–	50.0	70.0	20
	qua	22.0	23.0	3.1	0.9	14.0	17.0	27.0	12
	ros	26.8	8.0	3.1	–	–	21.0	35.0	20
Pharyngeal fibres, length	ba4	37.2	39.2	5.4	–	–	28.0	42.0	5
	bra	24.3	25.0	6.0	–	24.7	13.0	40.0	22

Table 31 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Pharyngeal fibres, length	pol	48.8	49.8	5.2	–	–	41.5	53.9	5
	ros	36.4	37.1	9.8	–	–	25.2	53.2	6
Macronuclear nodules, length	abb [e]	50.0	46.0	21.1	–	42.1	20.0	100.0	25
	ba1 [e]	20.0	21.0	6.0	1.5	29.8	11.0	34.0	15
	ba2 [f]	11.6	11.0	2.9	0.3	25.0	7.0	20.0	100
	ba3 [f]	14.0	15.0	4.1	0.6	29.0	7.0	26.0	40
	ba4	20.2	19.6	5.0	–	–	14.7	30.1	15
	bra [e]	12.9	11.0	4.8	–	37.1	6.0	24.0	36
	es1 [n]	13.3	13.0	2.1	0.5	15.8	10.0	19.0	22
	es1 [n]	12.4	12.0	2.0	0.4	15.5	9.0	16.0	22
	es2 [n]	13.6	13.0	3.0	–	22.2	7.0	21.0	24
	es2 [n]	12.7	12.5	2.7	–	21.1	7.0	20.0	24
	pol	14.3	14.5	3.7	–	–	7.5	23.2	20
	qua [f]	7.5	7.5	1.3	0.2	17.0	10.0 [c]	10.0	35
	ros [e]	7.7	7.7	1.4	–	–	4.9	11.9	20
Macronuclear nodules, width	abb [e]	5.2	5.0	1.2	–	23.8	4.0	8.0	20
	ba1 [e]	5.8	6.0	0.7	0.2	11.7	4.0	7.0	15
	ba4	7.2	7.7	1.0	–	–	5.6	8.4	15
	bra [e]	5.0	5.0	1.4	–	27.1	2.0	9.0	36
	es1 [n]	8.2	7.5	2.2	0.5	27.0	5.0	12.0	22
	es1 [n]	8.1	8.5	2.2	0.5	27.5	5.0	14.0	22
	es2 [n]	8.1	8.0	1.7	–	21.8	5.0	13.0	24
	es2 [n]	8.3	8.0	2.0	–	24.7	5.0	13.0	24
	pol	8.5	8.3	1.2	–	–	5.8	12.4	20
	ros [e]	5.6	5.4	1.3	–	–	4.2	9.1	20
Macronuclear nodules, distance in between	abb	12.2	9.0	8.7	–	71.7	3.0	38.0	20
	ba1 [o]	21.9	22.0	4.3	1.1	19.8	13.0	28.0	15
	bra [u]	10.5	10.0	3.6	–	34.2	4.0	17.0	37
	es1	14.1	14.0	3.3	0.7	23.6	9.0	20.0	22
	es2	12.1	11.0	5.2	–	42.8	6.0	26.0	25
	pol [u]	23.7	21.6	6.6	–	–	14.9	37.3	20
Micronucleus, length	ba1 [e]	2.9	3.0	0.2	0.5	7.4	2.3	3.0	15
	ba4	2.5	2.4	0.3	–	–	2.1	3.1	15
	bra	2.4	2.0	0.5	–	23.1	2.0	4.0	34
	pol	5.4	5.8	0.6	–	–	4.1	6.6	20
	ros	3.5	3.5	0.4	–	–	2.8	4.5	20
	es1 [n]	2.9	3.0	0.3	0.1	10.7	2.0	3.0	25
	es2 [n]	2.6	3.0	0.8	–	30.6	2.0	5.0	15
Micronucleus, width	ba4	2.3	2.1	0.3	–	–	2.1	2.8	15
	pol	4.3	4.1	0.5	–	–	3.3	5.0	20
	ros	2.8	2.8	0.5	–	–	2.1	4.2	20
Distance 1	ba1 [p]	22.4	22.0	3.7	0.9	16.3	15.0	29.0	15
Distance 2	ba1 [p]	15.4	15.0	1.4	0.3	8.8	13.0	18.0	15
Adoral membranelles, number	abb	21.4	21.0	1.7	–	8.0	19.0	26.0	20
	ba1	20.3	20.0	0.9	0.2	4.4	18.0	21.0	15
	ba2	19.0	19.0	1.2	0.2	6.0	18.0	22.0	29
	ba3	26.0	26.0	2.3	0.7	9.0	23.0	31.0	13
	ba4	21.0	21.0	1.5	–	–	19.0	24.0	15
	bra	21.9	22.0	2.2	–	9.9	18.0	31.0	45
	es1	30.3	30.0	1.5	0.3	5.0	28.0	33.0	22

Table 31 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Adoral membranelles, number	es2	29.4	30.0	2.9	–	9.9	20.0	34.0	23
	pol	43.3	43.0	2.2	–	–	39.0	48.0	20
	qua	22.0	23.0	2.4	0.7	11.0	5.5 [b]	27.0	12
	ros	17.0	17.0	1.1	–	–	14.0	18.0	20
Macronuclear nodules, number	abb	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	ba1	2.7	2.0	0.9	0.2	33.7	2.0	4.0	15
	ba2	4.0	–	–	–	–	3.0	5.0	29
	ba4	2.0	2.0	0.0	–	–	2.0	2.0	15
	bra	4.1	4.0	0.6	–	14.3	2.0	6.0	45
	es1 [n]	2.1	2.0	0.5	0.1	21.3	2.0	4.0	20
	es2	2.1	2.0	0.5	–	21.1	2.0	4.0	24
	pol	4.0	4.0	0.0	–	–	4.0	4.0	20
	qua	4.0	–	–	–	–	4.0	4.0	15
	ros	8.9	8.0	2.0	–	–	7.0	14.0	20
Micronuclei, number	abb	1.9	2.0	0.4	–	23.5	1.0	3.0	20
	ba1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
	ba4	2.7	2.0	0.7	–	–	2.0	4.0	15
	es1	2.2	2.0	0.4	0.1	17.3	2.0	3.0	25
	es2	2.0	2.0	0.6	–	27.8	1.0	4.0	16
	pol	1.7	2.0	0.4	–	–	1.0	2.0	20
	ros	1.6	1.5	0.7	–	–	1.0	3.0	20
Frontal cirri, number	abb	3.0	3.0	0.0	–	0.0	3.0	3.0	20
	ba1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	ba2 [t]	6.8	7.0	0.9	0.2	13.0	5.0	8.0	20
	ba3 [t]	6.0	6.0	1.3	0.4	22.0	4.0	9.0	13
	ba4	3.0	3.0	0.0	–	–	3.0	3.0	15
	bra	3.0	3.0	0.0	–	0.0	3.0	3.0	45
	pol	3.0	3.0	0.0	–	–	3.0	3.0	20
	ros	3.0	3.0	0.0	–	–	3.0	3.0	20
Buccal cirri, number	abb	1.2	1.0	0.4	–	34.2	1.0	2.0	20
	ba1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	ba4	1.0	1.0	0.0	–	–	1.0	1.0	15
	bra	1.0	1.0	0.0	–	0.0	1.0	1.0	45
	pol [v]	3.0	3.0	0.0	–	–	3.0	3.0	20
	ros	1.0	1.0	0.0	–	–	1.0	1.0	20
Parabuccal cirri, number	ba1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	ba4	1.0	1.0	0.0	–	–	1.0	1.0	15
	bra	1.4	1.0	0.5	–	38.8	1.0	3.0	44
	pol	8.9	9.0	1.1	–	–	6.0	11.0	20
	ros	1.0	1.0	0.0	–	–	1.0	1.0	20
Long cirral rows right of adoral zone, number [g]	abb	4.0	4.0	0.0	–	0.0	4.0	4.0	20
	ba1	6.0	6.0	0.0	0.0	0.0	6.0	6.0	15
	ba4	5.5	6.0	0.6	–	–	4.0	6.0	15
	bra	4.2	4.0	0.4	–	9.2	4.0	5.0	40
	es1 [l]	7.0	7.0	0.0	0.0	0.0	7.0	7.0	25
	es2	8.0	7.0	0.8	–	10.5	7.0	10.0	25
	pol	8.4	8.0	0.5	–	–	8.0	9.0	20
	ros	3.0	3.0	0.0	–	–	3.0	3.0	20
Cirral rows, total number	ba1 [d]	6.0	6.0	0.0	0.0	0.0	6.0	6.0	15
	ba2 [d]	9.4	10.0	0.6	0.1	6.8	8.0	10.0	32

Table 31 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Cirral rows, total number	ba3 [d]	6.0	6.0	0.8	0.2	12.0	5.0	8.0	11
	ba4	11.0	11.0	1.0	–	–	9.0	13.0	15
	pol	19.0	19.0	1.3	–	–	17.0	21.0	20
	qua [d]	11.5	11.0	0.8	0.2	7.0	10.0	12.0	12
	ros	6.0	6.0	0.0	–	–	6.0	6.0	20
Cirral rows on ventral side, number	qua	7.0	7.0	0.9	0.3	12.0	7.0	10.0	15
Cirri formed by anlage I, number	abb	1.0	1.0	0.0	–	0.0	1.0	1.0	20
	es1 [m]	6.0	6.0	0.5	0.1	8.4	5.0	7.0	21
	es2 [m]	5.8	6.0	0.9	–	15.7	4.0	7.0	24
Cirri formed by anlage II, number	abb	2.2	2.0	0.4	–	18.6	2.0	3.0	20
	es1 [m]	7.4	7.0	0.9	0.2	11.7	6.0	9.0	21
	es2 [m]	6.8	7.0	0.8	–	11.9	5.0	8.0	24
Cirri formed by anlage III, number	abb	5.0	5.0	1.6	–	31.8	3.0	10.0	20
	es1 [m]	16.0	16.0	1.9	0.4	12.0	13.0	20.0	20
	es2 [m]	15.0	16.5	3.6	–	24.4	9.0	20.0	24
Cirri formed by anlage IV, number	abb	18.7	19.0	2.3	–	12.1	15.0	25.0	20
	ba1 [q]	4.9	5.0	0.8	0.2	17.1	3.0	6.0	15
	ba4	4.0	4.0	0.6	0	–	3.0	5.0	15
	bra	20.2	21.0	6.4	–	31.7	10.0	34.0	40
	es1 [m]	24.7	24.0	2.5	0.6	10.2	22.0	32.0	18
	es2 [m]	22.2	22.5	4.7	–	21.1	10.0	32.0	24
	pol	34.1	34.5	2.5	–	–	30.0	38.0	10
Cirri formed by anlage V, number	abb	29.8	29.5	2.5	–	8.4	26.0	35.0	20
	ba1 [q]	13.7	14.0	2.1	0.5	15.6	10.0	17.0	15
	ba4	10.6	10.5	1.3	0	–	9.0	13.0	10
	bra	32.6	32.0	3.7	–	11.5	25.0	42.0	40
	es1 [m]	27.9	28.0	2.1	0.5	7.6	24.0	32.0	17
	es2 [m]	29.2	28.0	5.3	–	18.1	23.0	41.0	24
	pol	47.6	47.0	2.9	–	–	43.0	52.0	10
Cirri formed by anlage VI, number	abb	41.7	42.5	3.2	–	7.7	35.0	47.0	20
	ba1 [q]	33.1	33.0	4.0	1.0	12.1	25.0	38.0	15
	ba4	27.8	27.0	2.6	–	–	24.0	33.0	10
	bra	36.9	36.0	4.9	–	13.3	26.0	46.0	39
	es1 [m]	31.4	31.5	2.2	0.6	7.1	25.0	35.0	16
	es2 [m]	33.1	34.0	5.1	–	15.3	18.0	42.0	24
	pol	55.9	55.5	4.0	–	–	51.0	63.0	10
Left frontoventral row, number of cirri	ros [k]	14.0	14.0	2.0	–	–	11.0	14.0	20
Right frontoventral row, number of cirri	ros [k]	30.9	31.0	3.8	–	–	19.0	39.0	20
Right marginal row, number of cirri	abb [h]	43.2	43.0	4.4	–	10.2	37.0	52.0	20
	ba1 [r]	35.9	36.0	3.2	0.8	8.8	31.0	41.0	15
	ba4 [r]	23.4	23.0	4.1	–	–	16.0	32.0	10
	bra	36.7	35.0	6.7	–	18.3	26.0	52.0	38
	es1 [m]	27.8	27.0	2.0	0.6	7.1	25.0	32.0	12
	es2 [m]	35.9	36.0	3.7	–	10.4	29.0	43.0	24
	pol [w]	58.0	54.5	9.8	–	–	52.0	85.0	10
	ros	31.6	32.5	4.3	–	–	19.0	38.0	20
Middle right marginal row, number of cirri	ba1 [r]	30.0	30.0	3.2	0.8	10.8	25.0	38.0	15
	ba4 [r]	22.3	21.5	4.1	–	–	16.0	32.0	10
	es2 [m]	35.7	36.0	17.5	–	11.7	27.0	41.0	18
Outer right marginal row, number of cirri	ba1 [r]	21.3	22.0	2.6	0.7	12.4	18.0	25.0	15

Table 31 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Outer right marginal row, number of cirri	ba4 [r]	17.5	17.5	2.0	–	–	15.0	21.0	10
	es2 [m]	32.8	32.0	4.0	–	12.2	28.0	40.0	6
Cirral row R8, number of cirri [x]	pol	55.9	55.0	3.3	–	–	52.0	62.0	10
Cirral row R9, number of cirri [x]	pol	54.3	54.0	3.1	–	–	49.0	60.0	10
Cirral row R10, number of cirri [x]	pol	47.9	48.0	2.5	–	–	43.0	52.0	10
Cirral row R11, number of cirri [x]	pol	42.8	42.5	3.1	–	–	37.0	48.0	10
Cirral row R12, number of cirri [x]	pol	40.3	41.0	2.1	–	–	38.0	42.0	3
Left marginal rows, number	abb	3.0	3.0	0.2	–	7.5	3.0	4.0	20
	ba1	4.1	4.0	0.3	0.1	6.3	4.0	5.0	15
	ba4	5.1	5.0	0.7	–	–	4.0	7.0	15
	ba4	5.1	5.0	0.7	–	–	4.0	7.0	15
	bra	3.9	4.0	0.8	–	21.5	3.0	6.0	39
	es1	4.0	4.0	0.0	0.0	0.0	4.0	4.0	20
	es2	5.4	5.0	0.7	–	14.1	4.0	8.0	25
	pol	10.6	11.0	1.3	–	–	9.0	13.0	20
	ros	3.0	3.0	0.0	–	–	3.0	3.0	20
Left marginal row 1 [j], number of cirri	abb	30.1	30.0	2.6	–	8.7	26.0	36.0	20
	ba1	26.1	26.0	3.5	1.0	13.5	20.0	34.0	15
	ba4	21.1	20.5	2.5	–	–	18.0	25.0	10
	bra	29.5	29.0	5.5	–	18.6	17.0	41.0	40
	es1	17.9	19.0	1.8	0.5	9.9	14.0	20.0	15
	es2	18.3	19.0	4.1	–	22.6	11.0	26.0	23
	pol	35.2	35.5	1.1	–	–	34.0	37.0	10
	ros	24.1	23.5	1.8	–	–	22.0	28.0	20
Left marginal row 2 [j], number of cirri	abb	32.2	31.0	4.1	–	12.7	27.0	44.0	20
	ba1	23.7	24.0	2.6	0.7	11.0	18.0	28.0	15
	ba4	18.8	19.0	3.0	–	–	14.0	24.0	10
	bra	29.2	28.0	5.5	–	19.0	20.0	41.0	39
	es1	18.2	18.0	2.2	0.6	12.3	14.0	20.0	15
	es2	19.8	21.0	4.4	–	22.2	13.0	28.0	23
	pol	37.2	38.0	2.7	–	–	32.0	40.0	10
	ros	23.9	24.0	2.0	–	–	20.0	28.0	20
Left marginal row 3 [j], number of cirri	abb	37.4	37.0	3.5	–	9.5	31.0	44.0	20
	ba1	22.0	22.0	3.3	0.8	14.8	16.0	27.0	15
	ba4	18.4	17.0	2.5	–	–	16.0	23.0	10
	bra	30.5	28.0	7.1	–	23.3	19.0	48.0	39
	es1	21.9	22.0	1.8	0.4	8.1	19.0	25.0	17
	es3	22.1	23.0	3.8	–	17.1	15.0	31.0	23
	pol	36.8	37.0	2.1	–	–	32.0	40.0	10
	ros	24.3	24.0	.9	–	–	21.0	29.0	20
Left marginal row 4 [j], number of cirri	abb	30.0	–	–	–	–	–	–	1
	ba1	24.3	25.0	2.6	0.7	10.3	20.0	28.0	15
	ba4	18.4	18.0	3.1	–	–	15.0	24.0	10
	bra	26.3	27.0	4.3	–	16.5	13.0	34.0	25
	es1	24.5	24.0	3.2	0.8	13.1	20.0	32.0	17
	es2	24.8	24.0	3.8	–	15.4	19.0	33.0	23
	pol	37.6	38.5	3.7	–	–	32.0	43.0	10
Left marginal row 5 [j], number of cirri	ba4	19.7	19.0	2.9	–	–	16.0	25.0	10
	es2	27.9	27.0	4.6	–	16.6	20.0	37.0	23
	pol	37.1	36.5	2.5	–	–	34.0	41.0	10

Table 31 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Left marginal row 6 [j], number of cirri	ba4	21.0	21.0	–	–	–	2.0	2.0	1
	es2	29.6	31.0	5.2	–	17.6	22.0	36.0	7
	pol	37.7	37.0	3.4	–	–	33.0	44.0	10
Left marginal row 7 [j], number of cirri	ba4	19.0	19.0	–	–	–	19.0	19.0	1
	pol	40.8	4.0	3.3	–	–	36.0	46.0	10
Left marginal row 8 [j], number of cirri	pol	42.7	42.0	2.4	–	–	39.0	47.0	10
Left marginal row 9 [j], number of cirri	pol	42.3	43.0	3.2	–	–	37.0	47.0	10
Left marginal row 10 [j], number of cirri	pol	42.4	41.5	1.8	–	–	41.0	46.0	110
Left marginal row 11 [j], number of cirri	pol	40.4	39.0	3.5	–	–	36.0	45.0	7
Left marginal row 12 [j], number of cirri	pol	42.0	42.0	0.0	–	–	42.0	42.0	2
Left marginal row 13 [j], number of cirri	pol	45.0	–	–	–	–	–	–	1
Cirri in outermost cirral row, length	ros	12.0	12.6	1.1	–	–	9.8	14.0	15
Dorsal kineties, number	abb	2.0	2.0	0.0	–	0.0	2.0	2.0	20
	ba1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	ba2	1.0	–	–	–	–	–	–	20
	ba4	1.0	1.0	0.0	–	–	1.0	1.0	15
	bra	2.0	2.0	0.3	–	12.7	1.0	2.0	32
	es1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	es2	2.0	2.0	0.0	–	0.0	2.0	2.0	18
	pol	3.0	3.0	0.0	–	–	3.0	3.0	20
	qua	2.0	–	–	–	–	–	–	?
	ros	2.0	2.0	0.0	–	–	2.0	2.0	20
Dorsal kinety 1, number of basal body pairs	abb	20.6	21.5	3.0	–	14.5	16.0	26.0	20
	ba1	16.9	17.0	2.3	0.6	13.7	14.0	24.0	15
	ba4	15.4	15.5	1.4	–	–	12.0	17.0	10
	bra	21.6	21.0	4.2	–	19.3	13.0	28.0	41
	pol	28.2	28.0	3.0	–	–	22.0	32.0	10
	ros	14.0	14.0	1.4	–	–	11.0	17.0	20
Dorsal kinety 2, number of basal body pairs	abb	9.6	9.0	1.3	–	13.3	7.0	12.0	20
	bra	8.6	9.0	1.6	19.1	5.0	12.0	12.0	38
	pol	33.5	34.0	2.4	–	–	30.0	36.0	10
	ros	2.1	2.0	0.3	–	–	2.0	3.0	20
Dorsal kinety 3, number of basal body pairs	pol	22.5	22.5	1.6	–	–	20.0	25.0	10
Dorsal bristles, length	pol	2.1	2.1	0.3	–	–	1.7	2.5	10
	ros	3.6	3.5	0.6	–	–	2.4	4.2	15
Cyst, diameter (from life)	ba1	39.2	40.0	2.6	0.5	6.6	34.0	44.0	23

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known; if two values are known, then they are listed as Min and Max; if only one value is known, then it is listed as Mean), SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens, unless otherwise indicated.

[b] The value provided (5.5) is obviously incorrect.

[c] The value provided (10) is obviously incorrect.

[d] Dorsal kineties (invariable two) very likely not included in *D. quadrinucleata*. In (ba1) the number of cirral rows right of midline is given (starting with row formed by anlage IV). In (ba2) no specifications are made, and in (ba3) the number of "ventral rows" is given.

[e] Anterior (*D. rositae*), respectively, posterior (*D. abbrevescens*, *D. bacilliformis*, *D. brasiliensis*) macro-

Table 31 Continued

nuclear nodule measured. In *D. bacilliformis* (ba1) the posterior micronucleus was measured.

[f] Nodule (anterior? posterior?) not specified.

[g] Cirral rows which terminate behind level of buccal vertex.

[h] Designated as cirral row I7 by Eigner (1995).

[i] From life.

[j] Left marginal row 1 is the innermost row. In the redescription of *D. bacilliformis* by Berger & Foissner (1987) and the original description of *D. rositae*, "row 1" is the outermost left marginal row.

[k] Left frontoventral row designated as row 4 in original description of *D. rositae*; right frontoventral row designated as row 5 in original description of *D. rositae*.

[l] All rows right of adoral zone included (R1 to R7; Fig. 104k, l).

[m] In the original description and redescription of *D. estevesi*, the rows are designated as R1 to R7, that is, the values for R1 are listed under "Cirri formed by anlage I, number", those for R6 under "Cirri formed by anlage VI, number", and those for R7, R8, and R9 under "Right marginal row", "Middle right marginal row", and "Outer right marginal row". Note, however, that R1 (Fig. 104k) is very likely the cirral row formed by anlage II (= middle frontal cirrus plus buccal cirri); the left frontal cirrus is likely incorrectly included (my interpretation see Fig. 104n and text).

[n] From specimens with two, not bisected macronuclear nodules. The upper line of es1 and es2 refers to the anterior nodule, the lower line to the posterior nodule. For the micronucleus the diameter is given (es1, es2, bra).

[o] Distance between macronuclear pairs is given.

[p] Distance 1: distance between anterior end of cell and posterior end of frontoventral row IV (row 5 in Berger & Foissner 1987). Distance 2: distance between anterior end of cell and anterior end of frontoventral row V (row 6 in Berger & Foissner 1987). In Berger & Foissner (1987) distance 2 was incorrectly explained, namely, as distance between anterior end of cell and posterior end of frontoventral row V.

[q] Row IV is designated as "row 5" in Berger & Foissner (1987; Fig. 98g); row V = "row 6"; row VI = "row 7".

[r] "Right marginal row" is the inner right marginal row in *D. bacilliformis* (= "row 8" in Berger & Foissner 1987, Fig. 98g, h; "R7" in Küppers & Claps 2010); middle right marginal row = "row 9" in Berger & Foissner (1987) and "R8" in Küppers & Claps (2010); outer right marginal row = "row 10" in Berger & Foissner (1987) and "R9" in Küppers & Claps (2010).

[s] This is the "average", but sample size is not given.

[t] All enlarged cirri on frontal field counted, that is, enlarged cirri (e.g., buccal cirrus) behind true frontal cirri included.

[u] For *D. polycirrata* it is not indicated which distance was measured; in *D. brasiliensis* the distance between the two central nodules is given.

[v] Küppers & Claps (2010, Table 1) distinguished between buccal cirrus (rearmost cirrus of row II) and two cirri ahead of it.

[w] This row (= inner right marginal, supposed that row VI is the outermost frontoventral row) is row R7 in Küppers & Claps (2010). Further details, see Fig. 102b.

[x] For designation see Fig. 102b.

[y] The designation of the cirral rows is a difficult task in *Deviata*. See footnotes and figures for explanation. When you are uncertain, consult original papers.

Table 31a Comparison of four main features and specifics of *Deviata* species

Species	Number of [a]				Specific feature; type locality
	MA	AM	CR	DK	
D. abbrevescens (Fig. 96g, h)	2	21	7	2	Dorsal kinety 2 with widely spaced bristles posteriorly; sediment of pond, Austria
D. bacilliformis (Fig. 98e, f)	usually 2 or 4	19, 20	10, 11	1	One dorsal kinety; pond, Hungary
D. brasiliensis (Fig. 100a, b)	usually 4	22	12	2	Dorsal kinety 2 with large break in middle portion; sewage treatment plant, Brazil
D. estevesi (Fig. 104k, l)	usually 2	30	11	2	Contractile vacuole near midline; slightly saline lagoon, Brazil
D. polycirrata (Fig. 102b, c)	4	43	19	3	High number of cirral rows; temporary pond, Argentina
D. quadrinucleata (Fig. 99b, c)	4	23	11	2	Dorsal kinety 2 with inconspicuous break in middle portion; garden soil, Republic of Rwanda
D. rositae (Fig. 103b, c)	usually 8	17	6	2	Dorsal kinety 2 composed of two bristles only, usually eight macronuclear nodules; temporary pond, Argentina
D. spirostoma (Fig. 101a, b)	usually 4	45–50	8?	3	Dorsal bristles 8–12 µm long; freshwater, Azerbaijan

[a] Usually the median is given. References and more detailed values see Table 31. Abbreviations: AM = adoral membranelles, CR = long cirral rows (usually longer than adoral zone), DK = dorsal kineties, MA = macronuclear nodules.

***Deviata abbrevescens* Eigner, 1995**
(Fig. 96a–p, Tables 31, 31a, b)

1995 ***Deviata abbrevescens* nov. spec.**[1] – Eigner, Europ. J. Protistol., 31: 343, Fig. 1–16, Table 1 (Fig. 96a–p; original description; the slide [accession number: 1994/85][2] containing the holotype specimen [marked] and several paratype specimens is deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Aescht 2003, p. 379; 2008, p. 140).

1997 ***Deviata abbrevescens* Eigner, 1995** – Eigner, J. Euk. Microbiol., 44: 559, Fig. 13 (Fig. 96g, h; diagrammatic representation of cirral pattern and ontogenesis).

2001 ***Deviata abbrevescens* Eigner, 1995** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 17 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

[1] Eigner (1995) provided the following diagnosis: Size in vivo 100–320 × 18–40 µm. 4 long cirral rows right and 3–4 long cirral rows left of adoral zone of membranelles. Adoral zone of membranelles short, about the same length in small and large individuals. 2 connected macronuclear nodules, about 2/3 of body length. Basal body pairs of right dorsal kinety more widely spaced, usually containing 3 pairs of basal bodies in posterior half. Cirri composed of at least 4 basal bodies.

[2] According to Eigner (1995, p. 344), the accession number is 94/3.

2002 ***Deviata abbravescens*** – Lynn & Small, Ciliophora, p. 457, Fig. 53A, B (Fig. 96g, h; guide to ciliate genera; incorrect subsequent spelling; the illustrations are not from "Foissner 1995" as indicated by Lynn & Small 2002, but from Eigner 1995).

Nomenclature: The species-group name *abbrevescens* (from the Latin *abbrevescere*; becoming shorter) refers to the fact that the individuals become distinctly shorter before cell division (Eigner 1995). Type species of *Deviata* Eigner, 1995.

Remarks: Interestingly, Eigner (1995) did not compare *D. abbrevescens* with *Uroleptus elongatus* Fernandez-Leborans, 1981 (Fig. 97a, b) and *Perisincirra kahli* (Grolière, 1975) Jankowski, 1978 (Fig. 81a), type of *Perisincirra*, although all these species are very similar, inter alia, in body outline, size, nuclear apparatus, and infraciliature. *Deviata abbrevescens* and *P. kahli* can be separated by the number of cirral rows (7 in *D. abbrevescens* vs. 4 in *P. kahli*), the distance between the cirri within cirral rows (normal, that is, rather closely spaced vs. very widely spaced), and the number of dorsal kineties (2 vs. 3). For details on *U. elongatus* – classified as supposed synonym of *D. abbrevescens* – see page 574.

Deviata abbrevescens differs from *D. bacilliformis* mainly by the higher number of dorsal kineties (2 vs. 1), the lower number of cirral rows (7–8 vs. 10–11), and the higher number of basal bodies forming the somatic cirri (4 vs. 2). The morphology section below is based only on the rather detailed original description. For separation from other species, see key and Table 31a.

Morphology: Body size highly variable, that is, 100–320 × 18–40 µm in life. Body outline elongate; about 50% of specimens very slender, remaining more or less distinctly wider (Fig. 96a, b); anterior end tapered with tip left of midline, posterior end rounded. Pre-dividing specimens become shorter, but wider; however, without obvious changes in the cirral pattern. Body highly flexible and almost circular in cross section, that is, not flattened dorsoventrally (Fig. 96c). Invariable two very slender (length:width ratio 10:1 on average in protargol preparations; Table 31) macronuclear nodules, connected by thin thread; nuclear apparatus extends rather constantly over about two third of body length (Fig. 96a, b, h). Micronuclei about 5 µm across, usually one attached to each macronuclear nodule. Contractile vacuole, as is usual, close to left body margin at about 50% of body length. Cortical granules lacking. Cytoplasm with many grey granules 1–3 µm across and food vacuoles about 10 µm in diameter. Movement vermicular; when freely swimming it rotates clockwise about main body axis (Fig. 96e); sometimes *D. abbrevescens* is attached to the substratum with the anterior end, which then shows a flexible protrusion (Fig. 96d).

Adoral zone occupies 16% of body length on average with extremes ranging from 10% to 20% (Fig. 96a, g, Table 31; Eigner 1995); composed of an average of 21 membranelles of ordinary fine-structure. Buccal cavity inconspicuous because flat and narrow; obviously largely covered by distinct buccal lip (Fig. 96a). Undulating membranes almost straight to slightly curved, do not intersect optically, but slightly diverging posteriorly; paroral commences about at level of mid-endoral (Fig. 96g). I am uncertain whether the designation of the undulating membranes (endoral, paroral) is correct. Pharyngeal fibres extend obliquely backwards.

Cirral pattern rather constant in spite of the high number of rows; number of cirri within rows of usual variability (Fig. 96g, Table 31). All cirri about 10 µm long. Three slightly enlarged frontal cirri arranged in almost transverse pseudorow; right cirrus (homologous to cirrus III/3 of 18-cirri hypotrichs) usually slight displaced anteriad. Buccal cirrus right of anterior end of endoral. On average four parabuccal cirri behind right frontal cirrus; thus row III usually not extending beyond level of buccal vertex; second and third cirrus (from anterior) of this row obviously slightly enlarged. Frontoventral row IV begins slightly behind level of second cirrus (from anterior) of row III; extends to near cell centre (Fig. 96g). Frontoventral row V commences about at level of third cirrus of row IV, that is, about at 13% of body length in specimen show in Fig. 96g; ends usually more subterminally than frontoventral row VI and right marginal row. Frontoventral row VI commences close to distal end of adoral zone, terminates near rear body end. Right marginal row begins on dorsal side close to anterior end of cell, extends laterally and ventrally to near rear body end. Usually three, rarely four (one out of 20 specimens investigated) left marginal rows, which become longer anteriorly from inside to outside; outermost row extends on dorsolateral surface.

Dorsal bristles about 4 µm long, arranged in two kineties: Kinety 1 bipolar and with equally spaced bristles, kinety 2 posteriorly shortened and with widely spaced bristles in posterior half. Caudal cirri lacking (Fig. 96h).

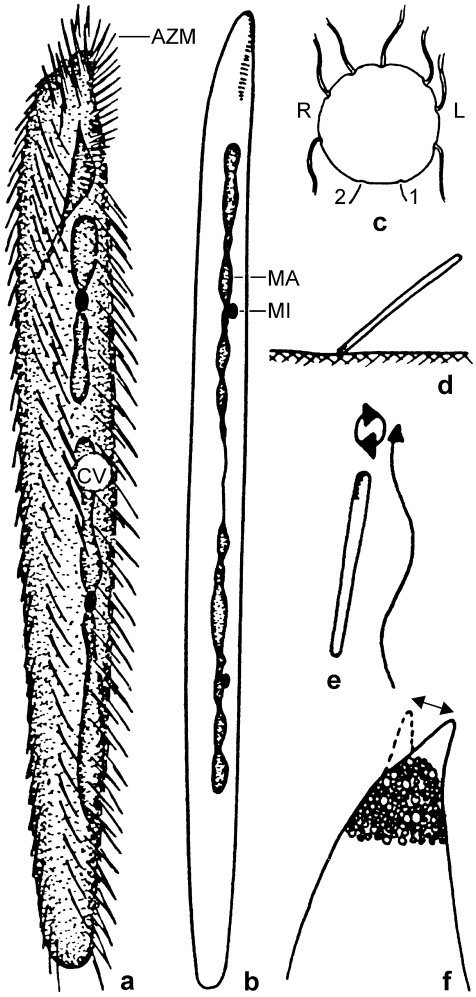


Fig. 96a–f *Deviata abbrevescens* (from Eigner 1995. From life). **a:** Ventral view of representative specimen, 172 µm. **b:** Ventral view of a very large and slender specimen, 295 µm. **c:** Cross-section in midbody (ventral side above) showing that *D. abbrevescens* is not flattened dorsoventrally. **d:** The cell is sometimes attached to the substratum with the anterior end. **e:** Movement is worm-like and rotation is clockwise. **f:** Colourless, flexible (double-arrow) protrusion at anterior end of cell, that is, the frontal scutum. AZM = adoral zone of membranelles, CV = contractile vacuole, L = left side of cell, MA = macronuclear nodule, MI = micronucleus, R = right side of cell, 1, 2 = dorsal kineties. Page 565.

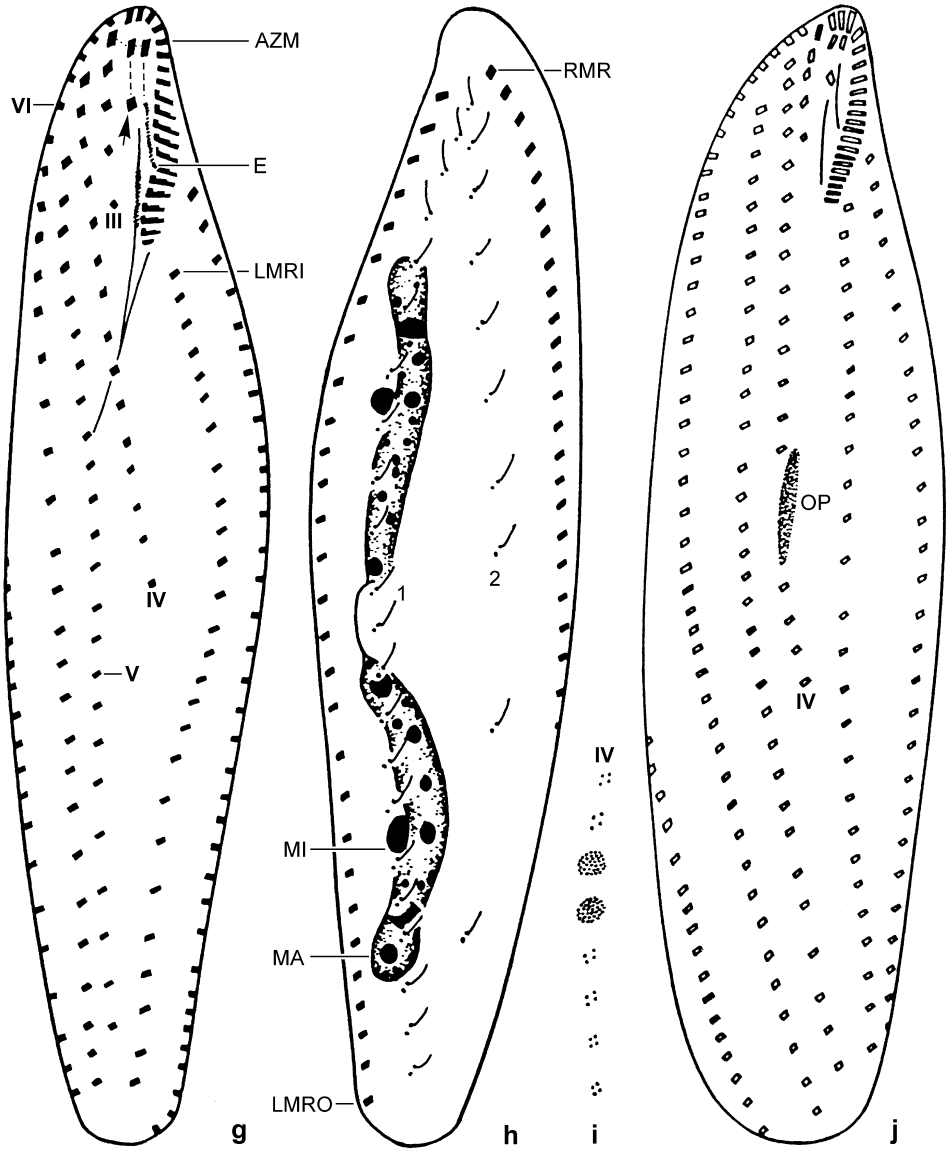


Fig. 96g–j *Deviata abbrevescens* (from Eigner 1995. Protargol impregnation). **g, h:** Infraciliature of ventral and dorsal side and nuclear apparatus of same(?) specimen, 129 µm. **i, j:** Some cirri in the rear portion of cirral row IV reshape to discoidal anlagen (i), which fuse to the oral primordium somewhat later (j), j = 177 µm. AZM = adoral zone of membranelles, E = endoral(?), LMRI = innermost left marginal row (= left marginal row 1), LMRO = outermost left marginal row, MA = macronuclear nodule, MI = micronucleus, OP = oral primordium, RMR = right marginal row, III–VI (bold) = cirral rows originating from anlagen III–VI (row III = I3 according to Eigner 1995; IV = I4; V = I5; VI = I6), 1, 2 = dorsal kineties. Page 565.

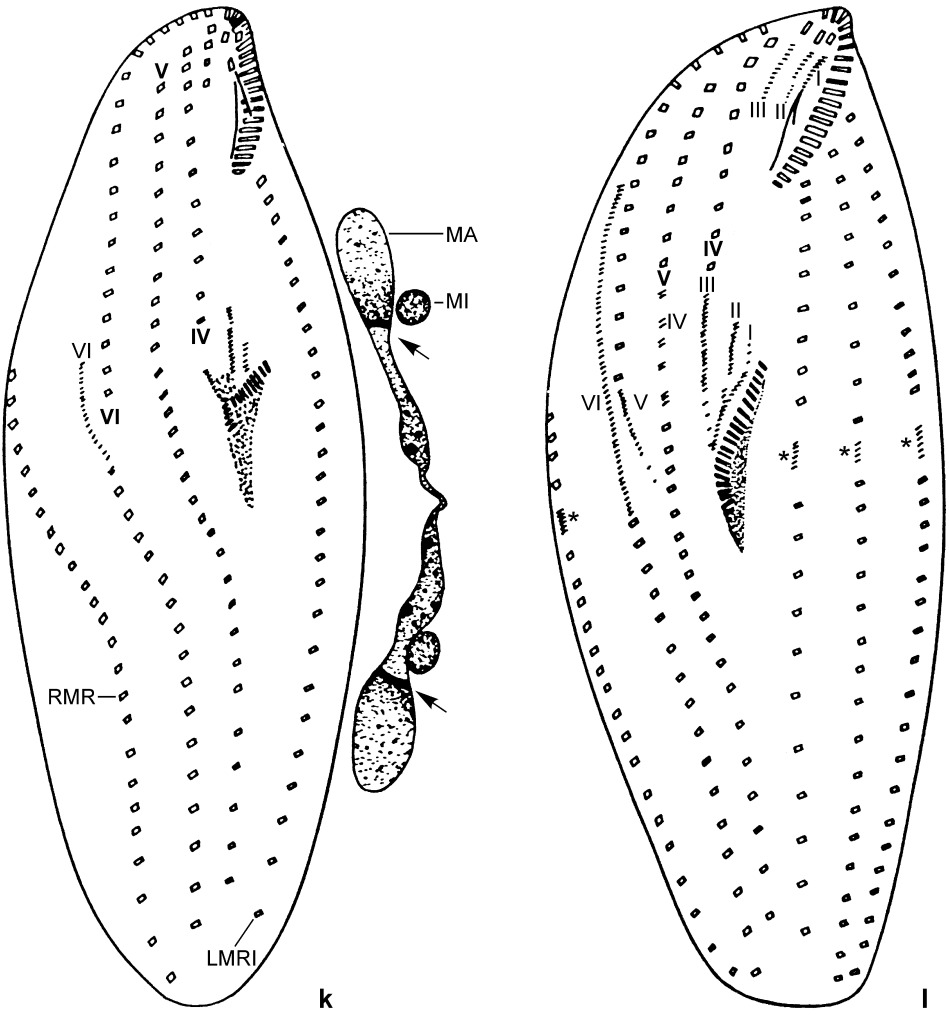
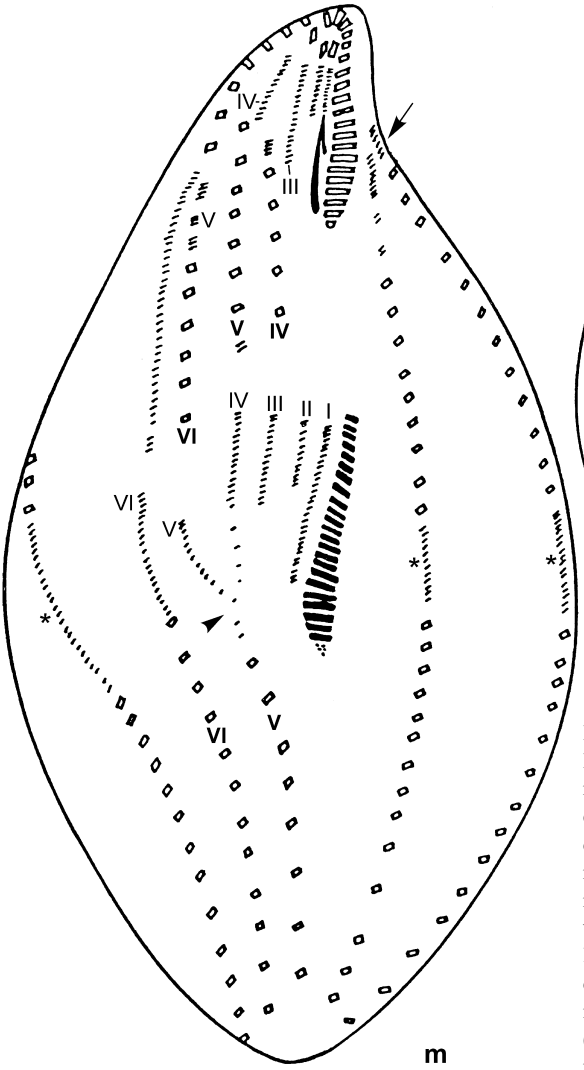


Fig. 96k, l *Deviata abbrevescens* (from Eigner 1995. Protargol impregnation. Parental structures white, new black). Infraciliature of ventral side and nuclear apparatus of early dividers, k = 165 µm, l = 153 µm. Note that anlage VI is a primary primordium. Further details, see text. Arrows in (k) mark replication bands. Asterisks mark anlagen in marginal rows of opisthe. LMRI = innermost left marginal row (= left marginal row 1), MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row, I–VI = parental cirral rows (bold), respectively, cirral anlagen (normal). Page 565.

Cell division (Fig. 96i–p): Morphogenesis of the ventral cirral pattern was studied in detail by Eigner (1995). He described six stages, showing that the process proceeds rather complicated. Especially the origin of the anlagen is difficult to follow (Table 31b). Thus, it is reviewed in detail, inasmuch *D. abbrevescens* is the type species of *Deviata*.



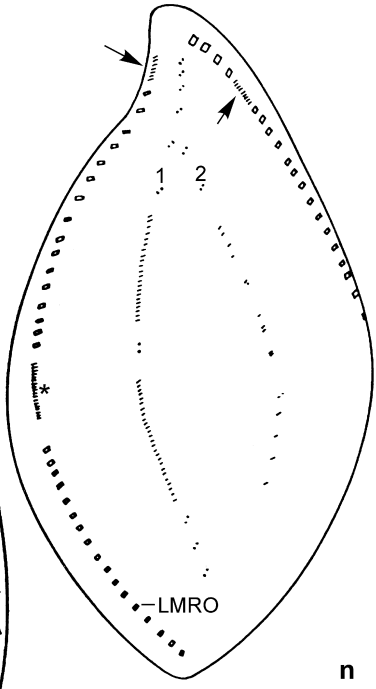


Fig. 96m, n *Deviata abbrevescens* (from Eigner 1995. Protargol impregnation. Parental structure white, new black). Infraciliature of ventral and dorsal side of middle divider, 140 µm. Asterisks: marginal row anlagen of opisthe; arrows: marginal row anlagen of proter; arrowhead: site where the anterior portion of opisthe's anlage V joins with parental row V. Further details, see text. LMRO = outermost left marginal row, I–VI = parental cirral rows (bold), respectively, cirral anlagen (normal), 1, 2 = dorsal kineties. Page 565.

Specimens which start to divide become wider and shorter, but show not cortical changes. When these pre-dividers have a body length:width ratio of about 3:1, the oral primordium begins to form from parental row IV, namely from the fifth and sixth cirrus from behind (Fig. 96i, j). The cirri reshape to discs, which is reminiscent of the situation in *Amphisiella* (Fig. 17q in Berger 2008). Whether the disc formation in these taxa is a homology or convergence is unknown. Somewhat later, the discoidal anlagen fuse to an elongate field, obviously by inclusion of some further cirri (Fig. 96j).

Next the oral primordium becomes roughly triangular differentiating membranelles in the left anterior portion (Fig. 96k). The anlagen I–III of the opisthe are

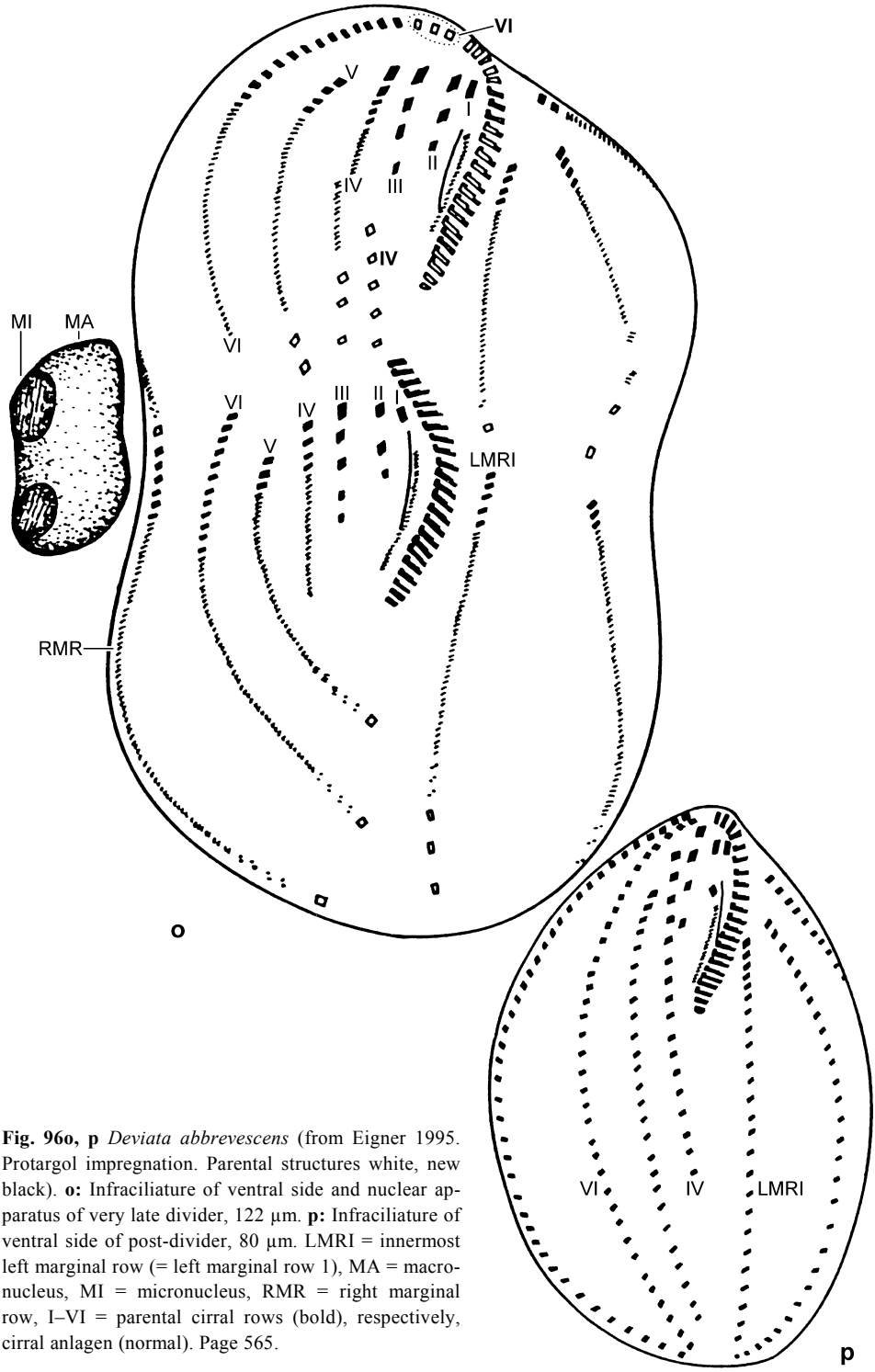


Fig. 96o, p *Deviata abbrevescens* (from Eigner 1995. Protargol impregnation. Parental structures white, new black). **o:** Infraciliature of ventral side and nuclear apparatus of very late divider, 122 µm. **p:** Infraciliature of ventral side of post-divider, 80 µm. LMRI = innermost left marginal row (= left marginal row 1), MA = macronucleus, MI = micronucleus, RMR = right marginal row, I–VI = parental cirral rows (bold), respectively, cirral anlagen (normal). Page 565.

formed, as is usual, from the oral primordium. Probably, some cirri of cirral row IV are incorporated in anlage III of the opisthe (Fig. 96l). At the level of the oral primordium, parental row VI opens by reshaping of one or two cirri to a primordium extending right of the anterior portion of row VI (Fig. 96k, l). This primordium becomes anlage VI in both filial products, that is, it is a primary primordium.

The adoral zone of the opisthe forms in posteriad direction (Fig. 96k). The posterior end of the anterior portion of the now bipartite parental row VI forms a streak extending towards parental row V. This streak becomes the anterior portion of opisthe's anlage V (Fig. 96l). Right of opisthe's anlage III, some cirri of parental row V reshape to opisthe's anlage IV (Fig. 96l). Anlagen I–III of the proter arise ordinarily, namely, (i) the anterior portion of the parental undulating membranes is modified to anlage I; (ii) one or two buccal cirri are reshaped to anlage II; and (iii) the parabuccal cirri are modified to anlage III.

In a middle divider, all adoral membranelles of the opisthe are formed and anlagen I–IV are more or less longitudinally arranged right of it (Fig. 96m). Anlage V of the opisthe, formed from the middle portion of parental row VI, separates from row VI and joins to the anterior end of the posterior portion of parental row V (Fig. 96m, arrowhead). The primary primordium VI bisects in an anterior portion which extends anteriorly to the parental row VI (according to Eigner 1995 this is the posterior portion of proter's anlage VI). The posterior portion of the primary primordium forms anlage VI of the opisthe. The anlagen I–III of the proter extend slightly. The anteriormost cirri of parental row IV reshape to a primordium, which extends obliquely backwards to the anterior end of the parental row V (Fig. 96m). According to Eigner (1995), this part becomes the anterior portion of proter's anlage IV. The anterior portion of the parental row VI splits and the anteriormost cirri of the resulting posterior part reshape to anlage V of the proter.

The undulating membranes originate by longitudinal splitting of anlagen I in both filial products (Fig. 96o); furthermore, the left frontal cirrus (I/1) is formed, as is usual, from the anterior portion of this anlage. Anlage II forms the middle frontal cirrus II/3 and one or two buccal cirri; anlage III forms the right frontal cirrus and the short frontoventral row or parabuccal row. Anlage IV of the proter becomes longer by involvement of cirri of parental row V. The cirri of the middle portion of the parental row IV are resorbed, while anlage V of the porter becomes longer in posteriad direction by incorporation of further cirri of parental row VI. In contrast, anlage VI of the proter lengthens anteriorly by incorporation of cirri of parental row VI (Fig. 96o). In postdividers all parental cirri which were not used for primordia formation, are resorbed (Fig. 96p).

The marginal rows develop in the ordinary manner, that is, by intrakinetal proliferation within each row at two levels (Fig. 96l–o). Eigner (1995) described and illustrated only one stage of dorsal morphogenesis (Fig. 96n). The anlagen develop within the parental kineties. The bristles of kinety 2 are very widely spaced posteriorly (Fig. 96h). Likely for that reason, the development of the anlagen in kinety 2 is

Table 31b Origin of the frontal-ventral cirri primordia in two *Deviata* species

Species (References)	Primordium [a]					
	I	II	III	IV	V	VI
Proter						
Deviata abbrevescens (Eigner 1995)	anterior portion of PUM	buccal cirrus/cirri	parabuccal cirri	anterior portion originates from anteriormost cirri of row IV; later, cirri of row V are involved	anterior portion of row VI splits and the anterior cirri of the resulting posterior portion become anlage V; later it becomes longer posteriorly by incorporation of cirri of row VI	anterior portion of the PP originating from middle portion of row VI
Deviata brasiliensis (Siqueira-Castro et al. 2009)	anterior portion of PUM	buccal cirrus	parabuccal cirri	anterior region of row IV	anterior region of row V	anterior portion of PP originating from middle part of row VI
Opisthe	I	II	III	IV	V	VI
Deviata abbrevescens (Eigner 1995)	OP	OP	OP (perhaps some cirri of row IV are involved)	some cirri of row V	anterior portion originates from posterior end of anterior portion of parental row VI; posterior portion originates from anterior end of posterior portion of parental row V	posterior portion of the PP originating from middle portion of row VI
Deviata brasiliensis (Siqueira-Castro et al. 2009)	OP	OP	row IV	? (row V)	? (row V or row VI)	posterior portion of the PP originating from middle part of row VI

[a] OP = oral primordium, PP = primary primordium, PUM = parental undulating membranes, ? = origin uncertain.

rather unusual according to Eigner (1995). Unfortunately, he did not provide a detailed explanation. Obviously no caudal cirri are formed.

The nuclear apparatus divides in the usual way, that is, the two macronuclear nodules fuse to a single mass and later divide into two nodules per filial product (Fig. 96h, k, o). Replication bands are present (Fig. 96k).

Occurrence and ecology: Limnetic. Type locality of *D. abbrevescens* is the village of Schrötten (46°47'N 15°49'E; 320 m altitude) near Deutsch Goritz, Austria, where Eigner (1995) discovered it at the bottom of a small, frozen pond. The sample was separated from most of the black mud and poured into a Petri dish. Local spring water (pH 7.41; 20 °C, $KMnO_4$ consumption 1.9 mg l^{-1}) was used a culture medium and squeezed wheat grains and baker's yeast were added to support bacterial growth. *Deviata abbrevescens* feeds on bacteria (Eigner 1995).

Supposed synonym of *Deviata abbrevescens*

Uroleptus elongatus Fernandez-Leborans, 1981
(Fig. 97a–c, Table 31)

1981 ***Uroleptus elongatus* n. sp.** – Fernandez-Leborans, Protistologica, 17: 5, Fig. 1–12 (Fig. 97a, b; original description of supposed synonym; no formal diagnosis provided; site where types deposited not mentioned).

1985 ***Uroleptus elongatus* Fernandez-Leborans 1981** – Fernandez-Leborans, Arch. Protistenk., 130: 372, Fig. 7, 17 (Fig. 97c; detailed description of undulating membranes).

2001 ***Uroleptus elongatus* Fernandez-Leborans, 1981** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 97 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: No derivation of the name is given in the original description. The species-group name *elongat·us, -a, -um* (Latin adjective [m: f; n]; elongate, stretched) very likely refers to the elongate body outline.

Remarks: Eigner (1995) obviously overlooked the description of *U. elongatus* and therefore did not compare *D. abbrevescens* with this species, which is mainly described after silver carbonate preparations where specimens inflate distinctly making an exact description of the infraciliature more or less impossible. Therefore, the cirral pattern is rather difficult to interpret (Fig. 97a) and shows, at the first glance, absolutely no similarity with that of *D. abbrevescens*. However, an extensive inspection reveals some relevant agreements between these two species: (i) limnetic habitat; (ii) number of adoral membranelles almost identical (21.4 on average in *D. abbrevescens* vs. 22 in *U. elongatus*); (iii) innermost cirral row in right body half terminates about in mid-body; (iv) four cirral rows in right body half; (v) bases of most cirri composed of four basal bodies (vs. two in *D. bacilliformis*). The rearmost two thirds of the outermost, that is, fourth left marginal row of *U. elongatus* are composed of basal body pairs, showing some resemblance with the left dorsal kinety of *D. abbrevescens*, inasmuch one cannot exclude that Fernandez-Leborans (1981)

made some misobservation on the heavily malformed specimens after silver carbonate impregnation. Noteworthy differences are the lack of the short frontoventral row formed by anlage III in *U. elongatus* and the location of the buccal cirrus (ahead of paroral in *D. abbrevescens* vs. distinctly behind anterior end of paroral in *U. elongatus*). Fernandez-Leborans (1981) described three more or less transversely arranged caudal cirri each composed of two basal bodies only, whereas *D. abbrevescens* lacks this part of the dorsal ciliature. Although it cannot be excluded that *U. elongatus* has indeed caudal cirri, I prefer the assumption that the rear portion of one of the outermost right marginal rows has been misinterpreted as caudal cirri. Because of this uncertainty I classify *U. elongatus* as supposed synonym of *D. abbrevescens*, that is, I keep the descriptions separate so that even taxonomists which do not accept this classification can use the review. When further studies (e.g., molecular comparison of populations from type localities) support my hypothesis, then *D. abbrevescens* becomes the junior synonym of *U. elongatus*, which has to be combined with *Deviata*. Another possibility is to declare *U. elongatus* as species indeterminata.

The original classification of the present species in *Uroleptus* Ehrenberg, 1831 is difficult to comprehend because species belonging to this taxon have a uroleptid midventral complex, that is, zigzagging ventral cirri with the right (= anterior) cirrus of each midventral pair usually distinctly larger than the left (= posterior) cirrus. Fernandez-Leborans (1981) compared *U. elongatus* only with *U. kahli* Grolière, 1975, which was fixed as type species of *Perisincirra* by Jankowski (1978). *Perisincirra kahli* can be separated from *U. elongatus* by the lower number of cirral rows (4 vs. about 8) and the higher number of dorsal kineties (3 vs. 1?). In addition, the marginal cirri of *P. kahli* are very widely spaced within the rows, whereas those of the present species are normally spaced (Fig. 97a). The wide spacing was confirmed by Foissner et al. (2002a) for two other *Perisincirra* species. Fernandez-Leborans (1981) used a terminology differing from the present one in some respects. The dorsal cirri in Fernandez-Leborans (1981) are the dorsal bristles; the left ventral cirri are the inner left marginal rows; the right ventral cirri are the two innermost cirral rows in the right body half; the right marginal cirri are the two outermost cirral rows in the right body half; the paroral kinety 1 is the endoral; the paroral kinety 2 is the paroral; and the buccal cirrus in the original description is likely the left frontal cirrus (cirrus I/1; see cell division).

Morphology: Body filiform, body length:width ratio of protargol-impregnated specimen figured about 8:1 (Fig. 1 in original description). Macronuclear nodules rather long and thin in protargol preparations, arranged in left body portion behind adoral zone. Number of micronuclei not mentioned; in specimen figured one close to anterior macronuclear nodule (Fig. 2, 3 in original description). Contractile vacuole, presence/absence of cortical granules, details about cytoplasm, and movement not mentioned.

Oral apparatus occupies only about 23% of body length, composed of circa 22 membranelles; adoral membranelles up to 4.7 µm wide. Individual membranelles of ordinary fine structure, those of middle portion composed of four kineties with

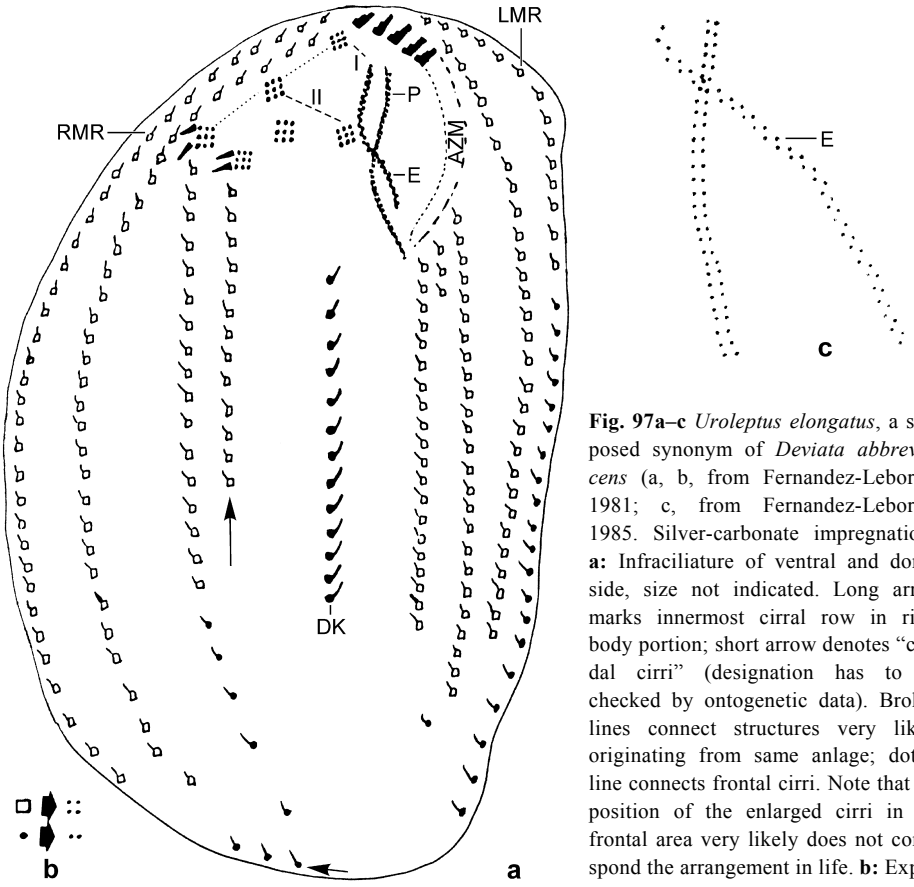


Fig. 97a–c *Uroleptus elongatus*, a supposed synonym of *Deviata abbrevescens* (a, b, from Fernandez-Leborans 1981; c, from Fernandez-Leborans 1985. Silver-carbonate impregnation). **a:** Infraciliature of ventral and dorsal side, size not indicated. Long arrow marks innermost cirral row in right body portion; short arrow denotes "caudal cirri" (designation has to be checked by ontogenetic data). Broken lines connect structures very likely originating from same anlage; dotted line connects frontal cirri. Note that the position of the enlarged cirri in the frontal area very likely does not correspond the arrangement in life. **b:** Explanation of cirral symbols used in (a). **c:** Undulating membranes. AZM = adoral zone of membranelles, DK = dorsal kinety (as seen from ventral side), E = endoral (paroral formation 1 according to Fernandez-Leborans 1981, 1985), LMR = outermost left marginal row (perhaps a misinterpreted dorsal kinety), P = paroral, RMR = (outermost) right marginal row, I, II = (supposed) frontal-ventral cirri anlagen. Page 574.

three, 10, 14, and 14 basal bodies; membranelles of anterior and posterior portion smaller. Peristome[1] size 21 × 11 µm. Exact arrangement of undulating membranes not known due to inflation, according to Fig. 97a, c optically intersecting. Paroral (= PK2 in original description) 15 µm long, composed of two parallel rows of 28 or 29 basal bodies each. Endoral (= PK1 in original description) 12 µm long, is a haplokinety made up of around 40–48 basal bodies (see also Fernandez-Leborans 1985).

Cirral pattern basically as in *D. abbrevescens* except for the cirral row behind the right frontal cirrus which is likely lacking in *U. elongatus*. Note, however, that the illustration shows a strongly inflated specimen after silver carbonate preparation so

[1] No explanation is given what the "peristome" exactly is.

that the correct arrangement of cirral rows is no longer recognisable (Fig. 97a). The following values refer to the specimen illustrated. Usually six (rarely seven or eight) enlarged cirri on frontal area: likely three frontal cirri; one buccal cirrus right of middle portion of undulating membranes (distinct difference to *D. abbrevescens*); and two cirri right of buccal cirrus (Fig. 97a; exact designation impossible because of displacement, perhaps parabuccal cirri). Frontal cirri, buccal cirrus, and cirrus III/2 usually composed of 3 × 3 basal bodies, bases about 1.3 µm long; bases of cirri composed of four basal bodies 0.6 µm long; bases of cirri composed of two basal bodies 0.4 µm long. Generally, size of cirri decreases from anterior (some cirri with 3 × 2 basal bodies) to posterior (often only two basal bodies). For some sophisticated details on the fibres associated with the cirri, see original description. Outermost cirral row in right body half composed of 36 cirri (n = 1!), next row made of 33 cirri. Third cirral row from right slightly shortened anteriorly, anterior portion consists of 17 cirri made of four basal bodies and a posterior portion made of five basal body pairs. Innermost row in right body half composed of 13 cirri. Innermost left marginal row commences at rear end of adoral zone, composed of 20 cirri; next row begins somewhat more anteriorly, consists of 26 cirri. Third left marginal row composed of 29 cirri, commences, like outermost row, near anterior cell end. Outermost row bipartite, that is, anteriormost 14 cirri composed of four basal bodies, rearmost 20 cirri made of two basal bodies only (possibly this row is a dorsal kinety; see remarks). Transverse cirri obviously lacking, although Fernandez-Leborans (1981) could not exclude that the rear portion of the second row right from midline are transverse cirri.

Length of dorsal bristles (inexactly designated as dorsal cirri in original description) neither mentioned nor recognisable in the figures; presumably they are of ordinary length, that is, about 2–4 µm. Dorsal kinety of illustrated specimen in central body portion, composed of 13 basal body pairs. Perhaps the outermost left marginal row is also a dorsal kinety because the main portion is composed of basal body pairs. According to Fernandez-Leborans (1981), the present species has three caudal cirri composed of basal body pairs forming an oblique row at rear (ventral) end of cell. Whether or not these are caudal cirri cannot be decided definitely; I suppose not.

Cell division: Fernandez-Leborans (1981) found one middle divider in his protargol preparations (Fig. 11 in his paper). However, the micrograph and the description are not very informative. Accordingly, five cirral primordia are formed; the left frontal cirrus originates, as is usual, from the undulating membrane anlage (note that this cirrus is designated as buccal cirrus in the original description); and the adoral zone of the opisthe is formed by the oral primordium.

Occurrence and ecology: The type locality of the supposed synonym *Uroleptus elongatus* is a freshwater habitat (details not given) from the Parque del Oeste in the city of Madrid, Spain (Fernandez-Leborans 1981). No further records of *U. elongatus* published. Fernandez-Leborans (1981) added one wheat grain per 50 ml of water to cultivate this species.

Deviata bacilliformis (Gelei, 1954) Eigner, 1995
(Fig. 98a–w, Tables 31, 31a)

1954 ***Kahlia bacilliformis* n. sp.**[1] – Gelei, Acta biol. hung., 5: 316, Abb. 41 (Fig. 98a; original description; no formal diagnosis provided and likely no type material available).

1960 ***Kahliella bacilliformis* (von Gelei, 1954)** – Corliss, J. Protozool., 7: 275 (combination with *Kahliella* Corliss, 1960).

1974 ***Strongylidium bacilliformis* Gelei** – Stiller, Fauna Hung., 115: 15, Fig. 8B (Fig. 98a; combination with *Strongylidium*; guide to hypotrichs of Hungary).

1975 ***Strongylidium bacilliforme* (Gelei, 1954) comb. n.** – Stiller, Acta zool. hung., 21: 222, Abb. 3 (Fig. 98a; combination with *Strongylidium*).

1987 ***Kahliella bacilliformis* (Gelei, 1954) Corliss, 1960** – Berger & Foissner, Zool. Jb. Syst., 114: 197, Fig. 7–17, Table 3 (Fig. 98b–l; six slides [accession numbers: 1986/51–56] have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; details see nomenclature).

1995 ***Deviata bacilliformis* (Gelei, 1954) nov. comb.** – Eigner, Europ. J. Protistol., 31: 358, Fig. 43 (Fig. 98e; comparison with *D. abbrevescens* and combination with *Deviata*).

2001 ***Deviata bacilliformis* (Gelei, 1954) Eigner, 1995** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 40 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2003 ***Kahliella bacilliformis* (Gelei, 1954) Corliss, 1960** – Dragesco, Trav. Mus. Hist. nat. Gr. Antipa, 45: 22, Fig. 33–39, Tables 8, 9 (Fig. 98m–t; description of two Rwandan populations [Fig. 98m–r = "population I" characterised in Tableau 8; Fig. 98s, t = "population II" characterised in Tableau 9]; voucher slides likely deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria [Dragesco 2003, p. 7]).

2010 ***Deviata bacilliformis* (Gelei, 1954) Eigner, 1995** – Küppers & Claps, J. Euk. Microbiol., 57: 280, Fig. 20–27, Table 2 (Fig. 98u–w; description of Argentinean population).

Nomenclature: No derivation of the name is given in the original description. The species-group name *bacilliform·is*, *-is*, *-e* (Latin adjective [m; f; n]) is a composite of the Latin noun *bacill·um* (diminutive of *baculum*; rod, stick), the thematic vowel *-i·*, and the Latin *formis* (a species looking like another species). Obviously the name refers to the rod-shaped body. *Kahliella bacillifera* in Foissner & AL-Rasheid (2006, p. 5) is an incorrect subsequent spelling.

Kahlia is feminine (see p. 348), *Strongylidium* is neuter (Aescht 2001, p. 301). Thus, Stiller (1975) had to change the species-group name from *bacilliformis* to *bacilliforme*; when she made this combination for the first time (Stiller 1974) in her guide to Hungarian hypotrichs, she has overlooked to make this emendation.

Berger & Foissner (1987, p. 195) wrote that "one slide of each other species described" (including *Kahliella bacilliformis*) has been deposited in the collection of microscopic slides of the Upper Austrian Museum in Linz (LI). However, finally we have lodged six slides (see list of synonyms), which are obviously labelled as neotypes (Aescht 2003, p. 381; 2008, p. 145). According to ICZN (1999, Article 75.3), a neotype is validly designated only when there is an exceptional need and only when that need is stated expressly and when the designation is published. Since we

[1] Gelei (1954) provided the following diagnosis: 100 µ langes, 40 µ breites, walzenförmiges Tier mit primitiver Ziliatur: 10 Zirrenreihen mit ganz dünnen Elementen, nach links gedreht. Zwei besondere Frontalcirrenreihen. Schmales Frontalfeld mit einem Wirbelorgan aus 16 Membranellen. Eine kleine Adoralmembran und 4 Makronuklei mit 2 Mikronuklei; c. V. nicht verfolgt.

(Berger & Foissner 1987) neither stated the need nor published the designation, the "neotypes" of *K. bacilliformis* deposited in the museum in Linz are therefore definitively invalid; they are voucher slides.

The lack of important taxonomic data (exact cirral pattern on frontal area in present case) due to incomplete descriptions is a reason for neotypification (ICZN 1999, Article 75). However, since the collecting sites of the redescribed populations (Israel, Berger & Foissner 1987; Rwanda, Dragesco 2003; Argentina, Küppers & Claps 2010) are rather far away from the original type locality (Börzsöny mountains, northern Hungary), I do not fix one of the redescribed populations as neotype. Individuals from or at least near the original type locality should be studied and used for neotypification (ICZN 1999, Article 75.3.6). In the meantime, the description of the Israeli population should be considered as authoritative because it is the most detailed one.

Remarks: The present species was described by Gelei (1954) from life and after sublimate fixation; Bresslau's opalblue or nigrosin staining failed because the specimens burst. Thus, the cirral pattern of the type population is not described in every detail (Fig. 98a). Especially it is not known whether or not it has – like the Israeli and Argentinean population (Fig. 98e, g, v) – a short frontoventral row, a structure which is obviously lacking in the Rwandan populations (Fig. 98n, t). The information about the dorsal infraciliature is somewhat cryptic in the original description because Gelei (1954) wrote "Die Sinnesborstenreihe konnte ich nicht untersuchen, da in Bresslau-Präparaten alle Tiere ausnahmslos platzten" (translated: "I could not study the bristle row [singular!] because all animals burst in Bresslau preparations"). From the singular of the word "row" one can conclude that he knew that this species has only one dorsal kinety.

Gelei (1954) assigned the present species to *Kahlia* Horváth, 1932, however, without explanation. Later, it was transferred to *Kahliella* Corliss, 1960 for preoccupation of *Kahlia* Horváth. In 1975, Stiller transferred *K. bacilliformis* to *Strongylidium* Sterki, 1878 because the cirral rows are helically arranged. However, both the original description and the redescriptions show that the torsion is only marginally or even lacking. We redescribed this species and stated that it can be easily separated from the other species assigned to *Kahliella*, but did not take into consideration that it could belong to a different genus (Berger & Foissner 1987). Eigner (1995) recognised that the cirral pattern of *K. bacilliformis* is very similar to that of *Deviata abbrevescens*, type of *Deviata*. Thus, he transferred it to this genus, a classification which is more reliable than that in *Kahliella*. Morphogenetic data of *D. bacilliformis* and molecular analyses of both species are needed to get a better insight into the systematic relationships. For separation of *D. bacilliformis* from the type species, see key, Table 31a, and *D. abbrevescens*.

According to Hemberger (1982, p. 29), *Kahliella bacilliformis* is only a variety of *K. acrobates* (p. 354) because (i) the ventral cirri pattern is identical and (ii) because already Kahl (1932, p. 546) noted a conspicuous variability in the nuclear apparatus of *K. acrobates*.

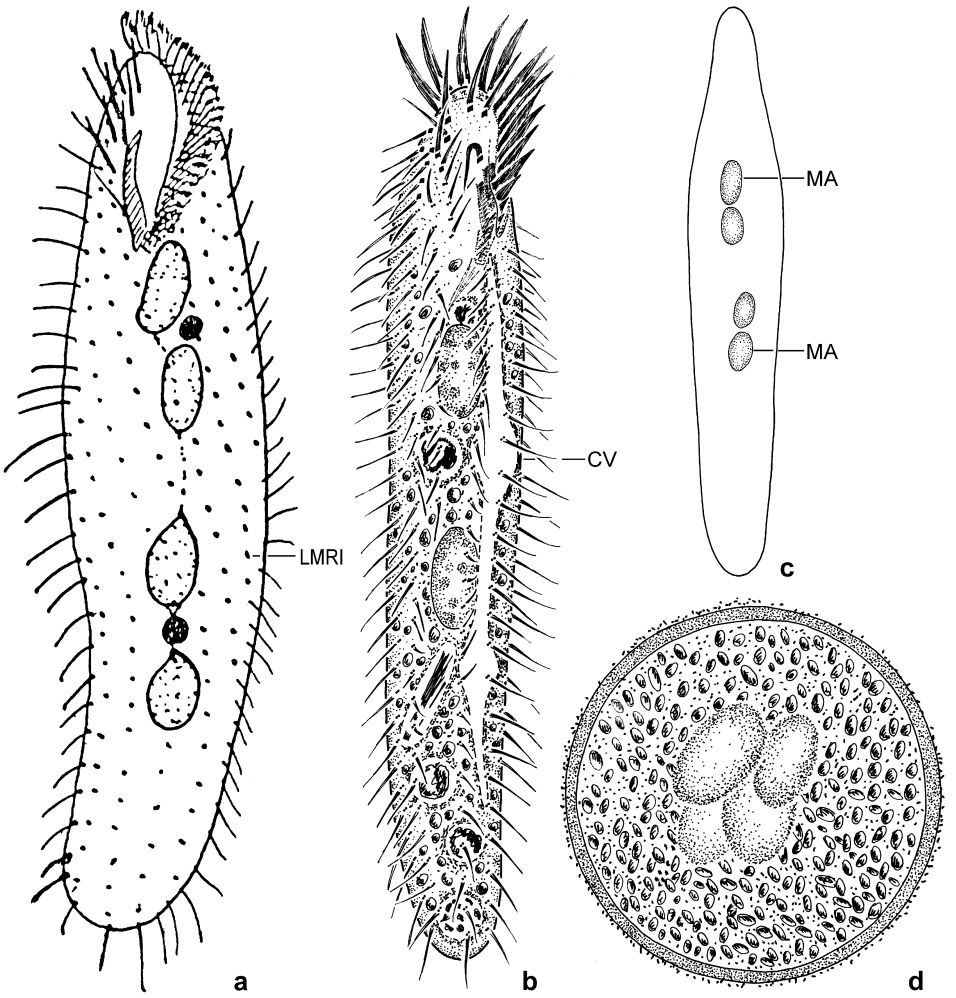


Fig. 98a–d *Deviata bacilliformis* (a, from Gelei 1954; b–d, from Berger & Foissner 1987. a, sublimate fixation; b–d, from life). **a:** Infraciliature of ventral side and nuclear apparatus, about 150 µm. **b:** Ventral view of representative specimen, 156 µm. **c:** Lateral view of specimen with four macronuclear nodules forming two distinct pairs, 165 µm. **d:** Resting cyst, diameter 42 µm. CV = contractile vacuole, LMRI = innermost left marginal row (= left marginal row 1), MA = macronuclear nodules. Page 578.

The population studied by Berger & Foissner (1987) agrees very well with the type material (Gelei 1954), especially in possessing 10 cirral rows and only one dorsal kinety. Gelei (1954) mentioned “two large double-nuclei (four macronuclei), with one micronucleus in between each pair”. By contrast, our population was dominated by specimens with two macronuclear nodules. However, it is not known how detailed the morphometry of the original description is. Altogether I am almost convinced that our Israeli population is conspecific with the population studied by Gelei (1954).

Dragesco (2003) investigated two populations, which differ from each other, inter alia, in body length (on average 132 µm vs. 194 µm) and the number of adoral membranelles (18 to 22 vs. 23–31; Table 31). As mentioned above, his populations obviously lack the short frontoventral row, and at least one population has two parabuccal cirri (Fig. 98n, p). Unfortunately, Dragesco (2003) did not provide details about the sample sites of these two populations. In addition, he erroneously assumed that the population studied by Berger & Foissner (1987) is from Europe.

The Argentinean population described by Küppers & Claps (2010) agrees very well with the type material and the population studied by Berger & Foissner (1987) and Dragesco (2003). Minor differences concern some details of the infraciliature. The total number of cirral rows is 9–11, sometimes 13 against 10 or 11 in the Israeli population, and the anteriormost basal body pairs of the outermost right marginal rows bear a bristle (Fig. 98u–w). In addition, Küppers & Claps (2010) invariably counted two macronuclear nodules, whereas Berger & Foissner (1987) found 2–4 nodules.

Uroleptus elongatus Fernandez-Leborans, 1981 is described only after silver-carbonate impregnation and therefore the exact cirral pattern is not known in detail. Preliminary it is classified as supposed synonym of *Deviata abbrevescens* because the bases of the ordinary cirri are composed of four basal bodies whereas those of *D. bacilliformis* are made

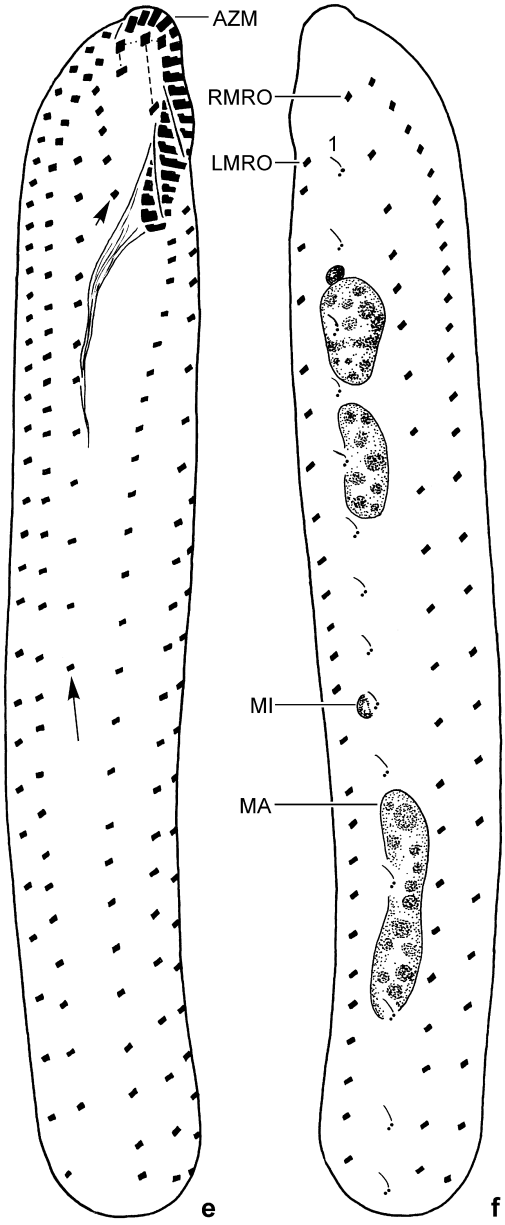


Fig. 98e, f *Deviata bacilliformis* (from Berger & Foissner 1987. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 121 µm. Short arrow: rear end of frontoventral row IV; long arrow: rear end of frontoventral row V. AZM = adoral zone, LMRO = outermost left marginal row, MA = macronuclear nodule, MI = micronucleus, RMRO = outermost right marginal row, 1 = dorsal kinety. Page 578.

up of only two basal bodies. In addition, the number of cirral rows is lower in *U. elongatus* and *D. abbrevescens* than in *D. bacilliformis* (7 or 8 vs. 10). By contrast, the single (value not quite certain) dorsal kinety of *U. elongatus* is reminiscent of *D. bacilliformis* (details see *U. elongatus*).

"*Kahliella bacilliformis* Gelei, 1954" sensu Fleury & Fryd-Versavel (1984) is likely a mixture of at least two species. For brief discussion, see p. 620. For separation of *D. bacilliformis* from other *Deviata* species, see key and Table 31a.

Morphology: At first the Israeli population studied by Berger & Foissner (1987) is described, followed by supplemental and/or deviating data from the type population (Gelei 1954), the African populations (Dragesco 2003), and the Argentinean population (Küppers & Claps 2010).

Body size of Israeli population about 115–170 × 25–40 µm (n = 4) in life. Body cylindrical, dorsoventrally flattened only in the oral region; anterior portion in ventral view slightly tapering, posterior one rounded or truncated (Fig. 98b, c). Macronuclear nodules usually two, about 20 × 9 µm in life, lying slightly left of median; sometimes one or both nodules bisected; chromatin bodies spherical, of very different size (Fig. 98b, f). Contractile vacuole close left body margin about in mid-body, during diastole with distinct collecting canals; systole occurs about every 60 s. Pellicle colourless, cortical granules lacking. Cytoplasm packed with about 2 µm large, spherical or ellipsoidal, colourless granules, 2–5 µm-sized globules, and many food vacuoles; hence, *Deviata bacilliformis* appears dark at low magnification. Sometimes a large defecation vacuole in posterior portion of cell. Movement rapid with rotation around main body axis, resembling a "holotrichous" ciliate.

Adoral zone occupies about 20% of body length, formed like a question mark, proximal third and buccal area covered by buccal lip; zone on average composed of 20 membranelles, bases of largest membranelles in life 5–6 µm wide. Undulating membranes straight to slightly bent, usually clearly separated, never optically intersecting, very probably formed by obliquely arranged basal body pairs; left basal body frequently less impregnated than right one; at present it is unclear which membrane is the paroral and which the endoral (Fig. 98b, e, g, i). Oral opening covered by buccal seal (Foissner & AL-Rasheid 1996, p. 5).

Cirral pattern and number of cirri of usual variability (Fig. 98e–l, Table 31). Cirri in life about 10–15 µm long. Three frontal cirri form transverse pseudorow, each consists of nine cilia. Buccal cirrus, parabuccal cirrus (= cirrus III/2), anteriormost one or two cirri of short frontoventral row, and anterior cirri of three rows right of short frontoventral row composed of four cilia each. All other cirri formed by two cilia only; from the posterior basal body an about 2 µm long, argentophilic fibre originates (Fig. 98j). Short frontoventral row terminates slightly ahead of level of buccal vertex on average. Next frontoventral row shortened anteriorly and posteriorly, begins at 13% and terminates at 55% of body length in specimen illustrated (Fig. 98e); right of this row four rows more or less of body length and outermost two rows extending on dorsal side (Fig. 98e–h). Usually four, rarely five left marginal

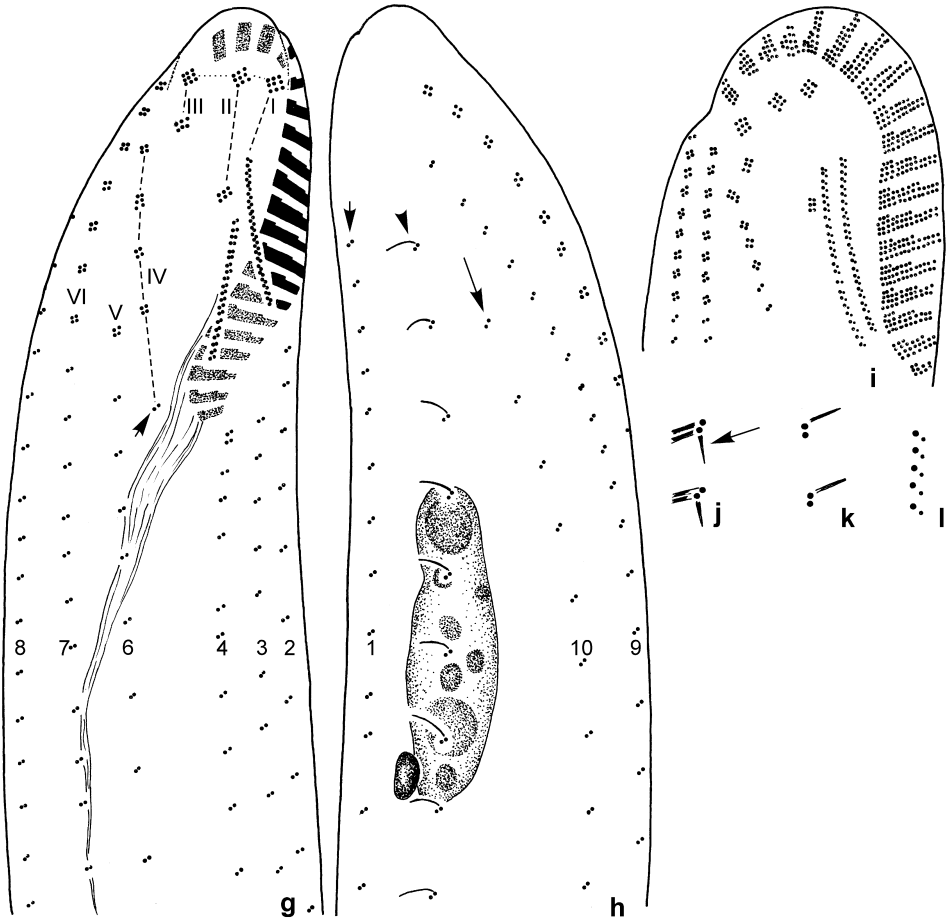


Fig. 98g–l *Deviata bacilliformis* (from Berger & Foissner 1987. Protargol impregnation). **g, h:** Infraciliature of anterior ventral and dorsal side of same specimen, 59 µm. Arrow in (g) marks rear end of frontoventral row formed by anlage IV. Arrowhead in (h) denotes dorsal kinety, short arrow in (h) marks outermost left marginal row, long arrow marks outermost right marginal row. Broken lines connect cirri originating from same anlage (only shown for anlagen I–IV); dotted line connects frontal cirri. **i–l:** Fine structure of adoral zone of membranelles (i), somatic cirral row (j; arrow marks argentophilic fibre), dorsal kinety (k), and an undulating membrane (l). I–VI = frontoventral rows originating from anlagen I–VI, 1–10 = numbering of cirral rows by Berger & Foissner (1987). Page 578.

rows, become slightly longer anteriorly from inside to outside; outermost row on dorsolateral surface.

Dorsal bristles about 3 µm long, invariably arranged in single kinety; caudal cirrus lacking (Fig. 98f, h, k).

Additional, deviating, and important data from type population (Gelei 1954; Fig. 98a): Body size 160 × 40 µm (in life?). Two large double macronuclear nodules, between each pair one micronucleus. Contractile vacuole inadvertently not observed.

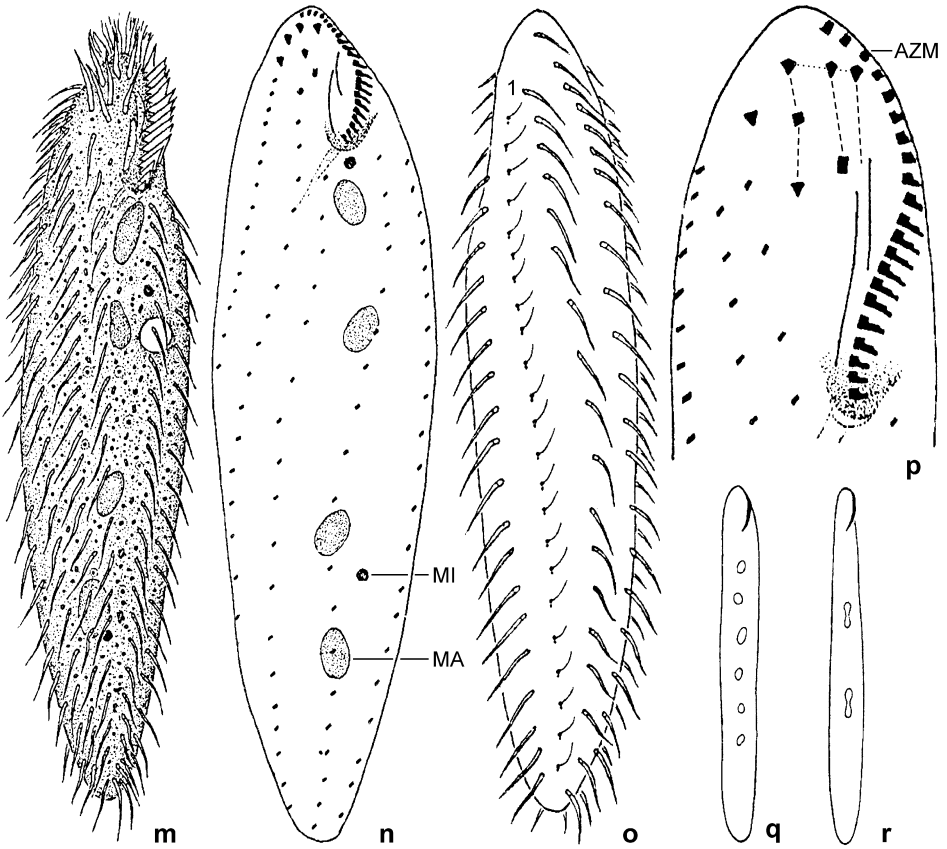


Fig. 98m–r *Deviata bacilliformis* (from Dragesco 2003. m, q?, r?, from life; n–p, protargol impregnation. "Population I" from near Kigali, Rwanda). **m:** Ventral view, size not indicated. **n, o:** Infraciliature of ventral and dorsal side, n = 141 µm, o = size not indicated. **p:** Infraciliature of oral region, 31 µm. Broken lines connect cirri originating from same anlage, dotted line connects frontal cirri. **q, r:** Variability of macronuclear apparatus. AZM = adoral zone of membranelles, MA = macronuclear nodule, MI = micronucleus, 1 = dorsal kinety. Page 578.

Body grey due to uniform, translucent "surface granules" ("Oberflächenkörnchen"); whether or not these granules are cortical granules is not known; the Israeli population had no cortical granules (Berger & Foissner 1987). Slowly moving. Adoral zone occupies 22% of body length in specimen illustrated (Fig. 98a), composed of about 26 membranelles (the 16 membranelles mentioned in the diagnosis [see footnote at list of synonyms] is likely a misspelling). Undulating membranelle (likely Gelei meant the paroral) composed of single row of cilia. Frontal cirri thicker than remaining cirri, but difficult to recognise because of dense arrangement. Gelei (1954) wanted to show in his illustration "that two special frontal rows (five frontal cirri) are present, whose two or three first cirri are somewhat closer arranged". 10 helical

cirral rows, cirri composed of a few cilia only. Transverse cirri and special ventral cirri lacking. One dorsal kinety (see remarks).

African populations described by Dragesco (2003; Fig. 98m–t, Table 31): Both populations obviously lack the short frontoventral row present in the Israeli and Argentinean population. Macronuclear nodules usually do not form distinct pairs (Fig. 98m, n, s, t). Population I (Fig. 98m–r) with 22 cirri on average in a non-specified ventral row (range given [19–20] obviously incorrect because maximum lower than average). Specimens shown in Fig. 98n, p with two parabuccal cirri (vs. invariably one in the Israeli and Argentinean population). According to Table 9 in Dragesco (2003), population II (Fig. 98s, t) has five dorsal kineties; I suppose that the dorsolaterally and dorsally arranged cirral rows are included.

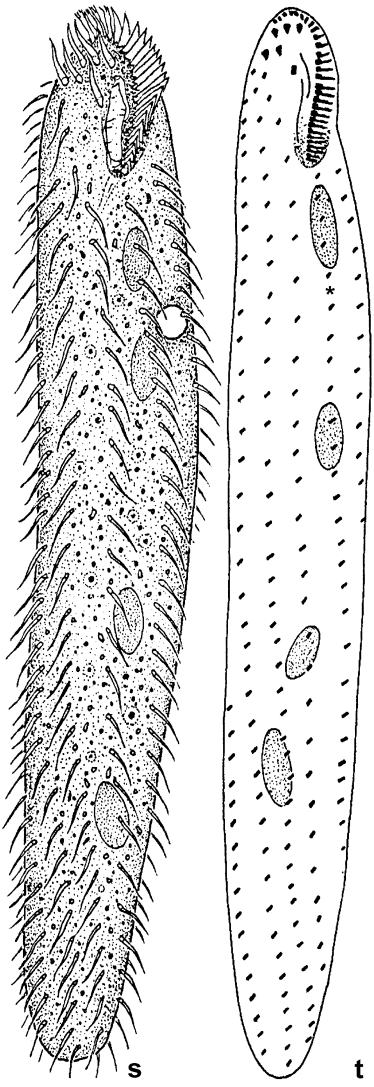


Fig. 98s, t *Deviata bacilliformis* (from Dragesco 2003. s, from life; t, protargol impregnation. "Population II"). **s:** Ventral view, 189 µm. **t:** Infraciliature of ventral side and nuclear apparatus, 182 µm. Page 578.

Argentinean population in life 65–154 × 35 to 70 µm (Küppers & Claps 2010). Body shape variable, that is, vermiform or slightly pyriform and wider, round in cross-section, but dorsoventrally flattened anteriorly (Fig. 98u). Uniformly two macronuclear nodules of variable shape (ellipsoidal, reniform, bilobed). 2–4 spherical or ellipsoidal micronuclei. Contractile vacuole near mid-body somewhat left of midline, during diastole with anterior and posterior collecting canal. Cytoplasm greyish-blackish at low magnification (<10×) due to inclusions. Cortical granules lacking. Adoral zone occupies on average 22% of body length in protargol-impregnated specimen, composed of 19–24 membranelles. For arrangement of cirri and variability, see Fig. 98v, w and Table 31. Frontal cirri composed of nine basal bodies (cilia), parabuccal cirrus made of six basal bodies. Cirral row IV commences about at level of parabuccal cirrus (= III/2), terminates slightly ahead of buccal vertex. 9–13 "long" cirral rows, that is, 4–6 right and 4–7 left of midline. Row V begins somewhat ahead of rear end of row IV and extends to 64% of body length in specimen illustrated (Fig. 98v). Anteriormost cirri of long rows composed mainly of four basal

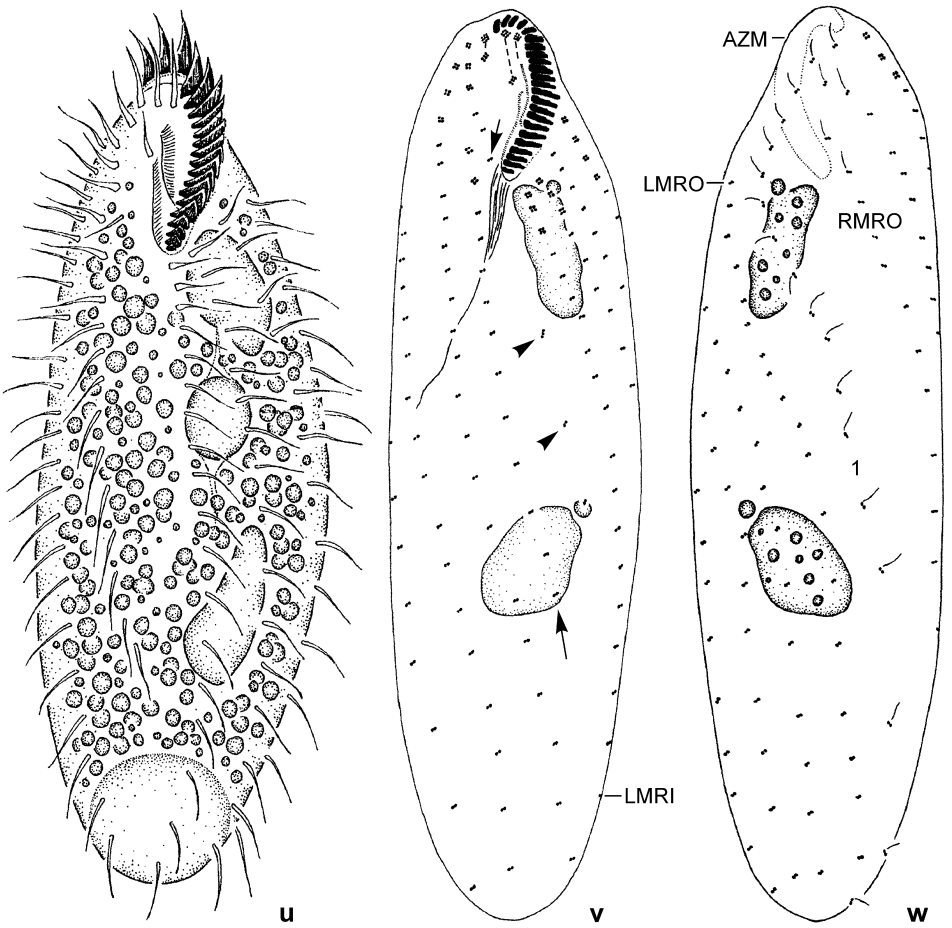


Fig. 98u–w *Deviata bacilliformis* (from Küppers & Claps 2010. u, from life; v, w, protargol impregnation). **u:** Ventral view, size of specimen not indicated (population 65–154 µm). **v, w:** Infraciliature of ventral and dorsal side and nuclear apparatus of same(?) specimen, 101 µm. Arrowheads in (v) mark barren basal bodies, short arrow marks rear end of frontoventral row IV, long arrow denotes rear end of row V. AZM = adoral zone of membranelles, LMRI = innermost left marginal row (= left marginal row 1; = row L1 in Küppers & Claps 2010), LMRO = outermost left marginal row (row L5 in Küppers & Claps 2010), RMRO = outermost right marginal row (= row R9 in Küppers & Claps 2010), 1 = dorsal kinety. Page 578.

bodies and therefore stouter than the remaining cirri, which are made of two basal bodies/cilia only. Two outermost right marginal rows with each two dikinetids in front of it with the anterior basal body bearing a dorsal bristle (Fig. 98c). Constantly one bipolar dorsal kinety, arranged in parallel to the outermost left marginal row.

Resting cyst (Fig. 98d): According to Berger & Foissner (1987), cysts are spherical and have a smooth, vitreous, about 1.5 µm thick wall. Less than 10% of the

population encysted under culture conditions. Cyst formation lasts several days as shown by the moving cytoplasm.

Cell division: Borror (1979a) made a general note that the frontal ciliature is restricted to a few cirri on the frontal field that develop from only two or three streaks. According to Küppers & Claps (2010), stomatogenesis commences with the (de novo?) formation of 1–3 pairs of non-ciliated basal bodies between cirral row V and inner left marginal row (Fig. 98v). Later, an elongated anarchic oral primordium occurs, likely without participation of parental row V.

In the type species of *Deviata*, the oral primordium originates within the parental cirral row IV (Fig. 96j). Likely due to the fact that this row terminates far ahead of the stomatogenic area, row IV is not incorporated in oral primordia formation in *D. bacilliformis*.

Occurrence and ecology: Limnetic and terrestrial; recorded from the Holarctic, Paleotropis, and Australis (Foissner 1998, p. 202). Type locality of *D. bacilliformis* is a temporary pond ("pond I") on a woody mountain pasture ("Csapásbérc") at the upper margin of the village of Diósjenő, Börzsöny Mountains, Hungary (Gelei 1954). The pond was used by pigs, sheep, goats, cows, and goose and therefore the loamy sediment was permanently poached up (further details on pond, see Gelei 1954a). Gelei (1954, p. 259) collected various samples, namely, (i) water, (ii) water plus sediment, (iii) dry sediment, and (iv) pond sediment dragged along on the embankment by the animals and which dried there. Unfortunately, Gelei (1954) did not specify in which sample type he discovered *D. bacilliformis*.

The population studied by Berger & Foissner (1987) is from the upper layer (0–5 cm) of a loamy soil of a wheat field near the village of Kibbitz, about 10 km south of Nazareth, Israel. It was cultured on Eau de Volvic enriched with squeezed wheat grains. The African population I described by Dragesco (2003, p. 22) is from (terrestrial?) mosses and *Sphagnum* habitats from/near the city of Kigali, Rwanda. Whether or not population II is from the same area is not mentioned. Küppers & Claps (2010) found *D. bacilliformis* in rewetted sediment samples from the dried bed of a temporary pond located near the city of Poblet, Buenos Aires Province (Argentina), collected during summers 2004 and 2005 (details on sample site and treatment, see Küppers et al. 2007). Further records of *D. bacilliformis*: two floodplain soils (humus type: typic mull) in Lower Austria east of Vienna, namely from the Müllerboden (*Pruno-Fraxinetum*) and the Beugenau (*Fraxino-Populatum*) area (Foissner et al. 2005, p. 626); *Sporobolus* girdle about 1 km off Etosha pan margin at the lookout "Etosha" and in a swamp around a spring at the Okerfontein water-hole in the Etosha National Park, Namibia (Foissner et al. 2002, p. 59a, sites 67 and 69).

Deviata bacilliformis feeds on short and long bacteria, volvocids (*Polytoma* sp.), and starch from the wheat grains added to the culture medium (Eau de Volvic; Berger & Foissner 1987; Foissner 1987a, p. 124). Gelei et al. (1954, p. 366) also reported bacteria as food for the type population. Biomass of 10^6 specimens 47 mg (Foissner 1987a, p. 124; 1998, p. 202).

Deviata quadrinucleata (Dragesco, 2003) comb. nov.
(Fig. 99a–c, Tables 31, 31a)

2003 ***Kahliella quadrinucleata* n. sp.** – Dragesco, Trav. Mus. Hist. nat. Gr. Antipa, 45: 23, Fig. 40–42, Tableau 10 (Fig. 99a–c; original description; no formal diagnosis provided; two slides with syntypes ([accession numbers: 2003/91, 2003/136; Aescht 2008, p. 175] have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; see Dragesco 2003, p. 7).

Nomenclature: No derivation of the species-group name is given in the original description. The name *quadrinucleata* is a composite of *quadr-* (Latin quantifier; four), the thematic vowel *·i-* (at the end of the first root, when the second begins with a consonant; Werner 1972), and *nucleat·us, -a, -um* (Latin adjective [m; f; n]; kernel-like) and obviously refers to the four macronuclear nodules.

Remarks: Dragesco (2003) classified the present species in *Kahliella* because the cirral pattern resembles that of *K. multiseta* (a junior synonym of *K. simplex* in present book), *K. microstoma* (a junior synonym of *K. acrobates*), and *K. acrobates*. This is basically correct, but there is an important difference in the dorsal kinety pattern not considered by Dragesco (2003). Unfortunately, the dorsal infraciliature of *K. acrobates*, type of *Kahliella*, is not known in detail. However, for *K. simplex*, possibly a junior synonym of the type species, the dorsal kinety pattern and its morphogenesis are described with modern methods. Accordingly, *Kahliella* has four dorsal kineties including one dorsomarginal row (Fig. 67f, 70k, o). By contrast, the present species has only two dorsal kineties of body length. In addition, it obviously lacks parental cirral rows with widely spaced cirri (Fig. 99a–c), a typical feature of *Kahliella* (e.g., Fig. 65f, g). As a consequence, I transfer *K. quadrinucleata* to *Deviata* whose type species also has only two dorsal kineties and lacks parental cirral rows (Eigner 1995). In addition, all species now assigned to *Deviata* have a rather short adoral zone of membranelles. A transfer of *K. quadrinucleata* to *Deviata* is also discussed by Küppers & Claps (2010, p. 282).

The most similar species is *D. brasiliensis* (see there for detailed comparison). *Deviata quadrinucleata* differs from the type species *D. abbrevescens*, inter alia, by the number of macronuclear nodules (4 globules vs. 2 connected, elongated nodules) and (long) cirral rows (about 11 vs. about 7), the body length and shape (around 100 µm and elliptical vs. 100–320 µm and rather slim), the structure of dorsal kinety 2 (roughly of body length with equally spaced bristles vs. distinctly shortened posteriorly and widely spaced bristles posteriorly), and the arrangement of the undulating membranes (Fig. 96g, 99b).

Dragesco (2003) found *Deviata bacilliformis*, which also has four macronuclear nodules, in the same region as *D. quadrinucleata*. However, these two species can be clearly distinguished by the number of dorsal kineties (one vs. two).

The description of *D. quadrinucleata* is not very detailed, that is, mainly composed of three illustrations and a brief morphometry (Fig. 99a–c, Table 31). Thus, some live data, for example, presence/absence of cortical granules, are not known. Consequently, description of further populations recommended. Morphogenetic data

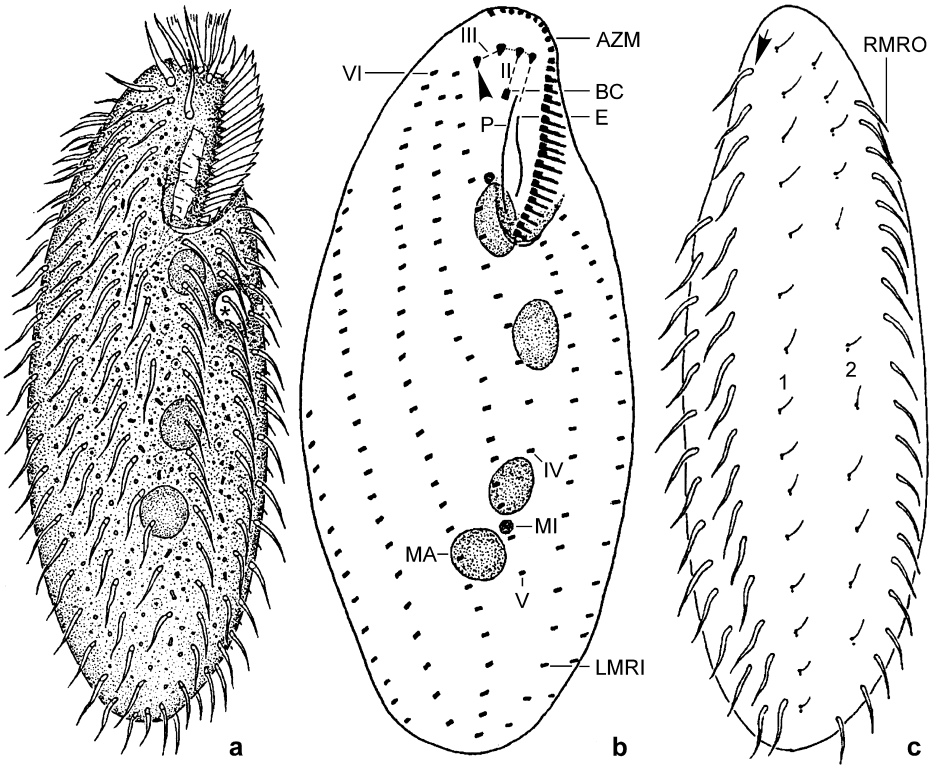


Fig. 99a–c *Deviata quadrinucleata* (from Dragesco 2003. a, from life; b, c, protargol impregnation). **a:** Ventral view showing, inter alia, contractile vacuole (asterisk) near left cell margin, 106 µm. **b:** Infraciliature of ventral side and nuclear apparatus, 100 µm. Arrowhead marks one of the five "frontal" cirri, which is, very likely, the cirrus (= cirrus III/2) behind the right frontal cirrus. Dotted line connects the three frontal cirri, broken lines connect cirri of anlagen I–III; note that ontogenetic data are needed to confirm or disprove my interpretation of the cirral pattern. **c:** Infraciliature of dorsal side, 105 µm. Arrow marks anterior end of outermost left marginal row. AZM = adoral zone of membranelles, BC = buccal cirrus, E = endoral, LMRI = innermost left marginal row (= left marginal row 1), MA = rearmost macronuclear nodule, MI = micronucleus, P = paroral, RMRO = outermost right marginal row, II–VI = frontoventral rows, 1, 2 = dorsal kineties. Page 588.

are needed for the correct interpretation (e.g., what are marginal rows?) of the cirral pattern. For separation from other *Deviata* species, see key and Table 31a.

Morphology: The original description of the present species is rather short. Thus, some important data are extracted from the illustrations provided. Body length (from life? after protargol impregnation?) 86–106 µm, ratio of body length:width of specimen shown in Fig. 99a about 2.7:1; body outline elliptical (Fig. 99a). Dorsoventral flattening not described, likely more distinct than in *Deviata abbrevescens*, which is almost circular in cross-section. Four globular macronuclear nodules arranged slightly left of midline in two more or less distinct pairs. Two micronuclei

(Fig. 99a, b). Contractile vacuole near left cell margin at about 36% of body length. Presence/absence of cortical granules, details on cytoplasm (colour, inclusions), and movement not described.

Adoral zone occupies about 31% of body length in specimen illustrated (Fig. 99b), on average only about 22% of body length and composed of 22 membranelles of ordinary fine structure (Table 31). Distal end of adoral zone at anterior end of cell, that is, zone does not extend onto right body margin. Buccal cavity rather small than large. Paroral slightly curved, longer than endoral; membranes roughly arranged in parallel (Fig. 99a, b).

Cirral pattern basically as in other *Deviata* species, that is, composed of several cirral rows some of which arranged on dorsal side. According to Dragesco (2003) five enlarged frontal cirri present, that is, very likely this species has (i) the ordinary three frontal cirri; (ii) one buccal cirrus right of the anterior end of the paroral; and (iii) one cirrus right behind the right frontal cirrus, indicating that this cirrus is homologous to cirrus III/2 (parabuccal cirrus) of other hypotrichs. Frontoventral row IV commences about at level of cirrus III/2, composed of 13 cirri and terminating at about 58% of body length in specimen illustrated (Fig. 99b); next row composed of 20 cirri, commencing about at level of buccal cirrus and terminating at 76%; remaining rows on right side roughly of body length (row VI composed of 31 cirri) and the outermost row(s) extending on dorsolateral side. Exact number of left marginal rows not given, according to Fig. 99b, c – which do not show the same individual – four left marginal rows are present, namely two on ventral side and two on dorsolateral side. No row with widely spaced cirri, indicating that rows of the previous generation(s) are not retained. Transverse cirri lacking.

Length of dorsal cilia not mentioned, according to Fig. 99c and scale bar about 3 µm. Bristles arranged in two rows in centre of dorsal side. Kinety 1 of specimen illustrated composed of 15 bristles. Kinety 2 somewhat shortened anteriorly and posteriorly and composed of 11 bristles; between fifth and sixth bristle an increased distance (whether this feature is individual- or species-specific is not known). Caudal cirri lacking.

Occurrence and ecology: Possibly confined to terrestrial habitats. Type locality of *D. quadrinucleata* is the garden of the University of Butare, Republic of Rwanda, where Dragesco (2003) discovered it in a soil sample. No further records published. Food not known.

Deviata brasiliensis **Siqueira-Castro, Paiva & Silva-Neto, 2009**
(Fig. 100a–m, Tables 31, 31a, b)

2009 ***Deviata brasiliensis*** **sp. nov.**[1] – Siqueira-Castro, Paiva & Silva-Neto, Zoologia, 26: 775, Fig. 21–27, Table II (Fig. 100a–m; original description. The slide [accession number IBZ 0007-3] containing the

[1] Siqueira-Castro et al. (2009) provided the following diagnosis: *Deviata* measuring about 110 × 45 mm (of course µm is meant) in vivo (n = 5). With three frontal cirri and one buccal cirrus distinctly isolated from the remaining ventral ciliature; with three to six long cirral rows left and 4–5 right of AZM. Row R4

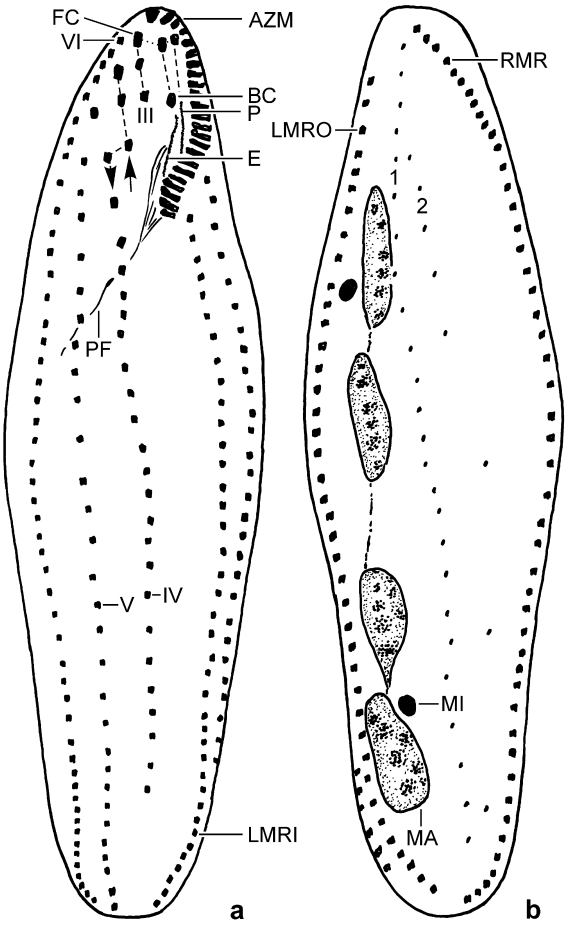


Fig. 100a, b *Deviata brasiliensis* (after Siqueira-Castro et al. 2009. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of same(?) specimen, 82 µm. Broken lines connect cirri originating from same anlage (only shown for anlagen I–IV). Forward pointing arrow marks misaligned cirrus in row IV. Note the fine threads connecting the macronuclear nodules, and the widely spaced basal body pairs in dorsal kinety 2. AZM = adoral zone of membranelles, BC = buccal cirrus, E = endoral, FC = frontal cirri, LMRI = innermost left marginal row (L1 in original description), LMRO = outermost left marginal row (L3 in original description), MA = rearmost macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = right marginal row (R7 in original description), III–VI = frontal and frontoventral rows (rows IV–VI termed R4–R6 in original description), 1, 2 = dorsal kineties. Page 590.

holotype and several paratypes is deposited in the collection of the Laboratório de Protistologia, Universidade Federal do Rio de Janeiro [UFRJ]).

Nomenclature: Siqueira-Castro et al. (2009) named this species after the country (Brazil, Brasil) where it was discovered.

Remarks: *Deviata brasiliensis* is very similar to *D. quadrinucleata* (Fig. 99a–c) so that synonymy cannot be excluded (see *D. quadrinucleata* for comparison with other species). However, because of a meticulous difference in the dorsal kinety pattern I preliminary accept both species, but further studies (investigation of more populations from/near the type localities, gene sequence analyses of reliable identified populations) will show which of the three possibilities (synonymy, subspecies, species) is the most

usually ends at about 4/5 of body length. On average with four macronuclear nodules of variable shape (viz. roughly ellipsoid, ovoid, fusiform or dumbbell-like). Ventral primordium V of the proter originates from anterior end of row R5.

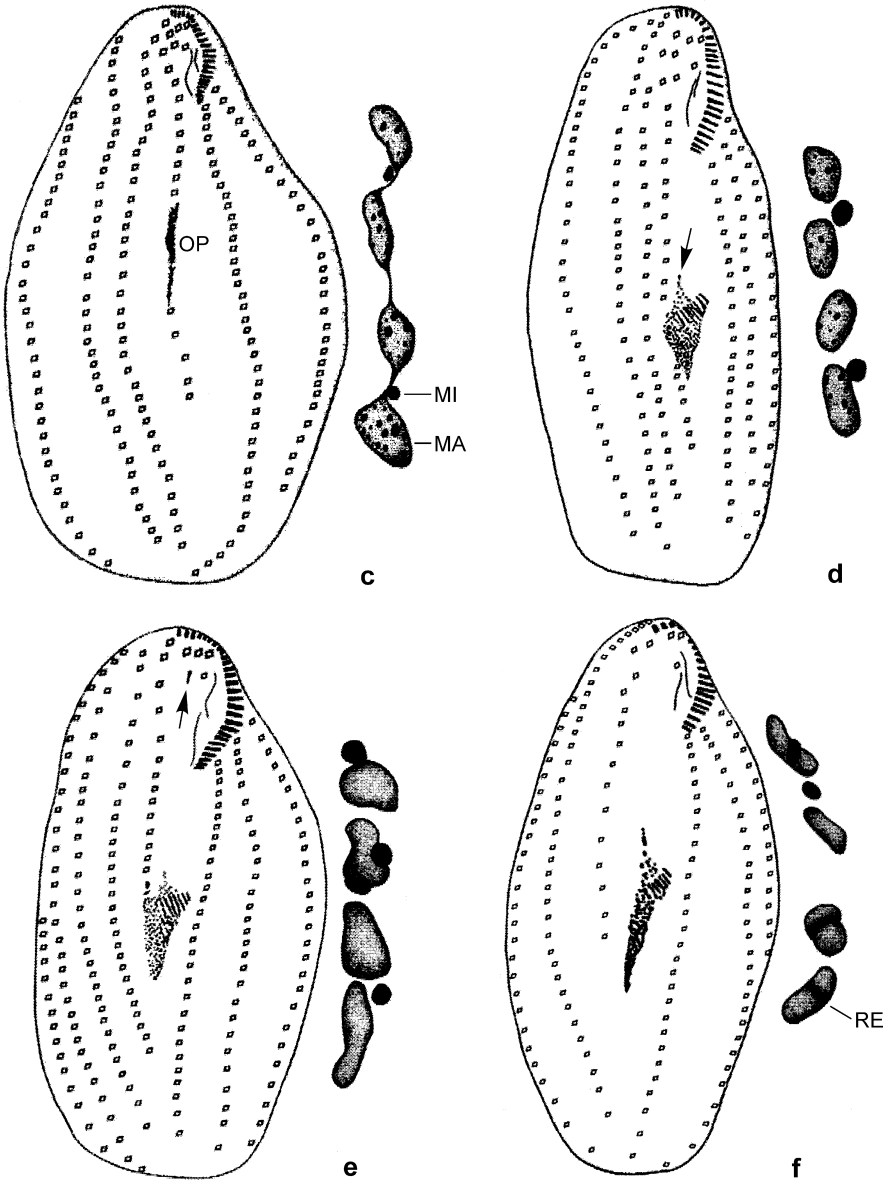


Fig. 100c–f *Deviata brasiliensis* (from Siqueira-Castro et al. 2009. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus of early dividers, c = 120 µm, d = 148 µm, e = 126 µm, f = 140 µm. Arrow in (d) marks undulating membrane anlage (= anlage I) of opisthe. Arrow in (e) denotes modified parabuccal cirrus, which forms anlage III of the proter. In the specimen shown in (f) the oral primordium obviously originates de novo, that is, without contact to parental ciliature. MA = macronuclear nodules, MI = micronucleus, OP = oral primordium, RE = Replication band. Page 590.

appropriate one. Kinety 2 of *Deviata quadrinucleata* commences, according to Fig. 99c, at the anterior cell end and has a distinct break slightly ahead of mid-body and the anterior and posterior portion are composed of normally spaced bristles. By contrast, kinety 2 of *Deviata brasiliensis* is distinctly shortened anteriorly and the bristles are very widely spaced in the middle and posterior portion (Fig. 100b).

At first glance *D. quadrinucleata* lacks parabuccal cirri (Fig. 99b). However, I suppose that the cirrus marked with an arrowhead is not a frontal cirrus, but the parabuccal cirrus (= cirrus III/2). Of course, further studies – including ontogenetic ones – are needed to show whether or not this assumption is correct. *Deviata brasiliensis* has 1–3 (median = 1.0) parabuccal cirri. Other quadrinucleate species have only one dorsal kinety (*D. bacilliformis*; vs 2 in present species) or twice as much adoral membranelles and three dorsal kineties (*D. polycirrata*, *D. spirostoma*). For comparison with other *Deviata* species, see key and Tables 31, 31a.

Morphology: Body size about 110 × 45 µm in life (n = 5). Body outline elongate elliptical with pointed anterior end. Body only indistinctly flattened dorsoventrally, that is, almost circular in cross-section; flexible and slightly contractile. 2–6, on average four macronuclear nodules arranged in two pairs in left body portion; individual nodules connected by fine threads that impregnate with protargol. Individual nodules highly variable, that is, roughly ovoid, ellipsoidal, fusiform, or dumbbell-shaped. 2–4 spherical micronuclei (Fig. 100b). Contractile vacuole about in mid-body, close to left cell margin. Cells dark at low magnification, likely because cytoplasm moderately densely filled with compact crystals, which are, however, less conspicuous than those in *D. estevesi*. Cortical granules absent. Movement not described, likely without peculiarities.

Adoral zone occupies 19% of body length and composed of 22 membranelles on average (Table 31); roughly shaped as in *Gonostomum* (Fig. 100a). Undulating membranes as in *D. estevesi* according to Siqueira-Castro et al. (2009), that is, arranged roughly in parallel, rarely intersecting optically with end of paroral slightly ahead of that of endoral. Pharyngeal fibres extend obliquely backwards.

Cirral pattern basically as in type species (Fig. 100a, b). Number and arrangement of cirri of usual variability (Table 31). Frontal cirri only slightly larger than remaining cirri, roughly arranged in transverse pseudorow immediately behind distal membranelles. Buccal cirrus close to anterior end of undulating membranes. 1–3 parabuccal cirri. Four or five long cirral rows right of adoral zone; leftmost long frontoventral row composed of 10–34 cirri, usually shortened posteriorly, that is, terminating about at 80% of body length; rarely this row ends about in mid-body or close to rear cell end; in one specimen this row terminates at about 35% of body length (Fig. 26 in original description). In about 60% of the specimens investigated, the anterior cirri of the leftmost frontoventral row were misaligned, sometimes feigning an extra row running parallel to its anterior portion. Seldom two isolated, barren kinetids (dikinetids?) in postoral region (Fig. 27 in original description). 3–6 left marginal rows, outermost row – like outermost right cirral row – dorsolaterally arranged (Fig. 100a, b, Table 31). Transverse cirri lacking.

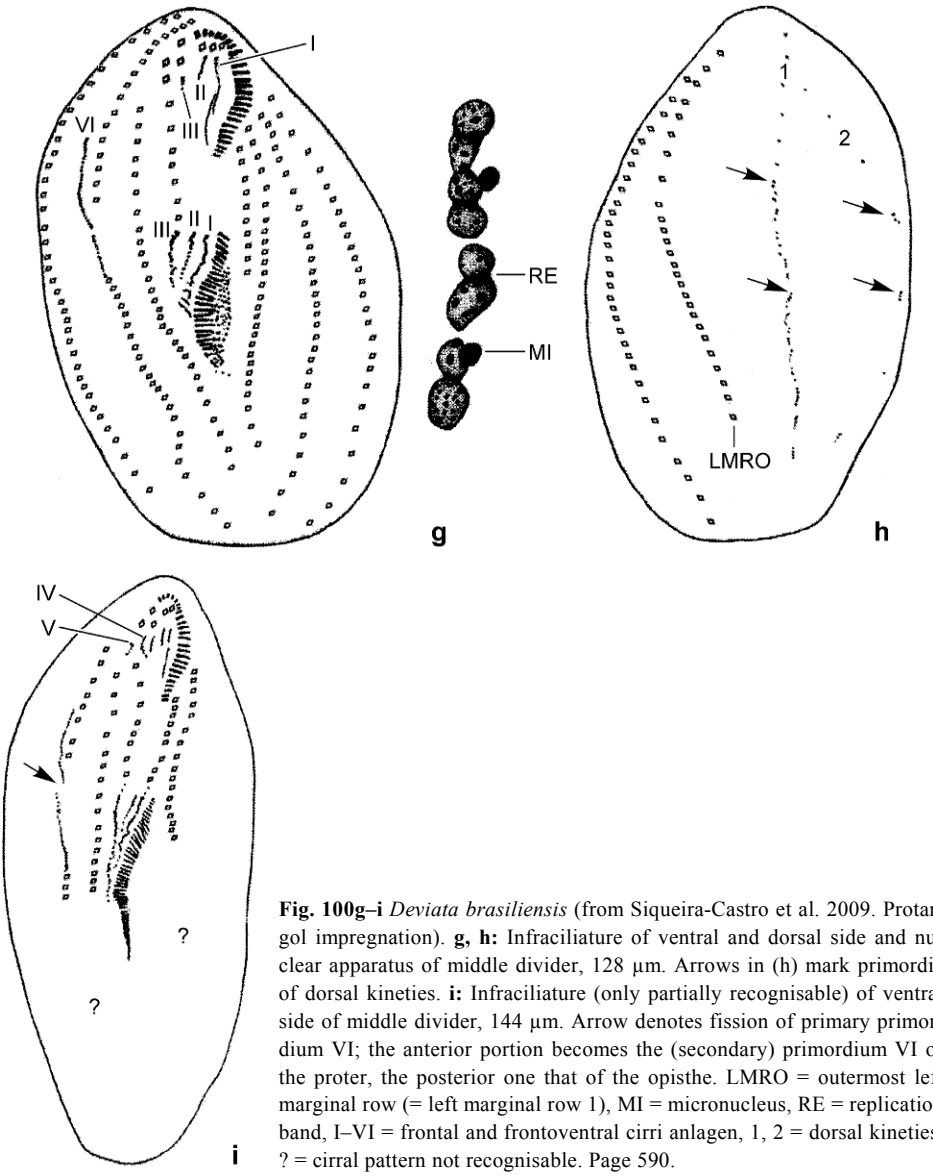


Fig. 100g–i *Deviata brasiliensis* (from Siqueira-Castro et al. 2009. Protargol impregnation). **g, h:** Infraciliature of ventral and dorsal side and nuclear apparatus of middle divider, 128 µm. Arrows in (h) mark primordia of dorsal kineties. **i:** Infraciliature (only partially recognisable) of ventral side of middle divider, 144 µm. Arrow denotes fission of primary primordium VI; the anterior portion becomes the (secondary) primordium VI of the proter, the posterior one that of the opisthe. LMRO = outermost left marginal row (= left marginal row 1), MI = micronucleus, RE = replication band, I–VI = frontal and frontoventral cirri anlagen, 1, 2 = dorsal kineties, ? = cirral pattern not recognisable. Page 590.

Almost invariably two dorsal kineties (Fig. 100b, Table 31). Bristles in kinety 1 about equally spaced. Kinety 2 distinctly shortened anteriorly, at least in specimen illustrated, bristles of anterior portion normally spaced, those of middle and rear third widely spaced. Length of bristles not described, according to Fig. 25 in the original description they are short, that is, about 2–4 µm. Caudal cirri lacking.

Cell division (Fig. 100c–m): This part of the life cycle is described relatively detailed in the original description (Siqueira-Castro et al. 2009).

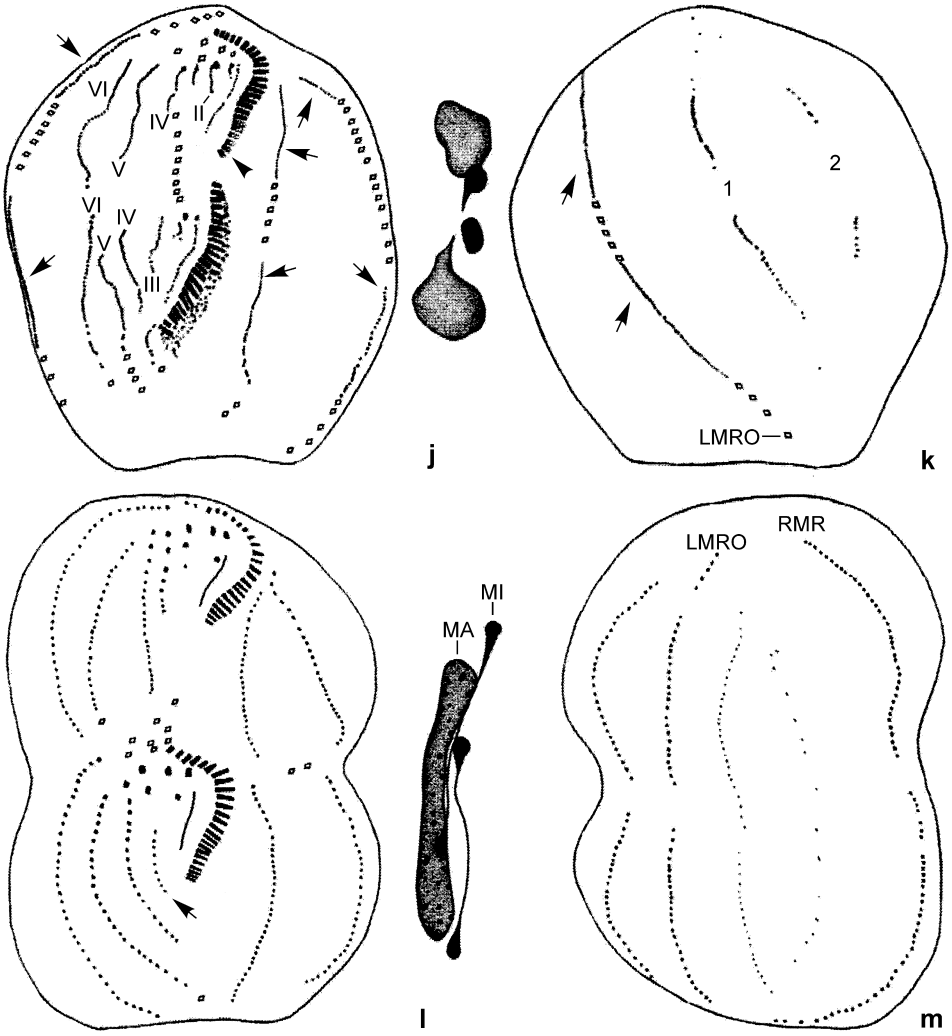


Fig. 100j–m *Deviata brasiliensis* (from Siqueira-Castro et al. 2009. Protargol impregnation). **j, k:** Infraciliature of ventral and dorsal side and nuclear apparatus of late divider, 110 µm. Arrowhead marks (probably) reorganising adoral membranelles. Arrows denote marginal row anlagen. **l, m:** Infraciliature of ventral and dorsal side and nuclear apparatus of very late divider, 128 µm. Arrow marks a cirral row which is, according to the original description, likely a fragment of primordium IV and may explain the misaligned pattern found in some specimens. LMRO = outermost left marginal row, MA = dividing macronucleus, MI = dividing micronucleus, RMR = right marginal row, I–VI = frontal-ventral cirri anlagen, 1, 2 = dorsal kineties. Page 590.

Morphogenesis commences with the formation of an oral primordium within the parental leftmost frontoventral row (Fig. 100c). The oral primordium enlarges, inter alia, by the incorporation of cirri of this row (Fig. 100d, e). In one specimen the oral

primordium was located in the area between leftmost frontoventral row and innermost left marginal row, indicating that the primordium originated de novo (Fig. 100f); however, it cannot be excluded that the rearmost cirrus of the leftmost frontoventral row was involved in the formation of the primordium (Siqueira-Castro et al. 2009). In the opisthe, anlagen I and II originate from the oral primordium, while anlage III seemingly is formed from the leftmost frontoventral row (Fig. 100g; has to be checked). Siqueira-Castro et al. (2009) could not unambiguously determine the origin of anlagen IV and V. They proposed the following possibilities: (i) both anlagen originate from the rear portion of row V, or (ii) anlage IV develops from row V and anlage V from row VI. At first, anlage VI is, as in *D. abbrevescens*, a long primary primordium originating from row VI; later, it splits and forms the anlagen VI for proter and opisthe.

Primordium I of the proter is formed, as in many hypotrichs, from the anterior portion of the parental undulating membranes, while anlage II originates from the buccal cirrus and anlage III from the parabuccal cirri. Anlagen IV and V are formed from the anterior portions of rows IV and V, respectively (Fig. 100i).

Within the parental marginal rows two anlagen are formed (Fig. 100j, k). The two dorsal kineties originate in the ordinary way, that is, within each row two anlagen occur, the anterior for the proter, the posterior for the opisthe (Fig. 100h, k, m). No caudal cirri are formed at the rear end of the dorsal kineties.

Very likely no parental ciliature (except adoral zone) is retained in postdividers. Siqueira-Castro et al. (2009) found one specimen where the proximal membranelles of the parental adoral zone were reorganised (Fig. 100j). The parental undulating membranes disorganised and became the undulating membrane anlage (= anlage I) of the proter only in middle and late dividers.

The nuclear apparatus divides as in most other hypotrichs, that is, replication bands develop and the nodules fuse to a single mass, which later divides into the species-specific number of nodules (Fig. 100c–g, j, l).

The morphogenesis of *D. brasiliensis* agrees well with that of *D. abbrevescens* (type of *Deviata*) in the formation of the oral primordium and the anlagen I–III and VI (Table 31b). By contrast, the formation of anlagen IV and V is more complicated in *D. abbrevescens* than in *D. brasiliensis*. At present it is difficult to interpret these differences, that is, it is uncertain whether or not the two species belong to the same genus. Perhaps relevant molecular data can provide further information in this respect.

Occurrence and ecology: Type locality of *D. brasiliensis* is a sewage treatment plant (Estação de Tratamento de Esgotos da Penha, ETE-Penha, Companhia Estadual de Águas e Esgotos [CEDAE/RJ]), located in the district of Penha, Rio de Janeiro, state of Rio de Janeiro, Brazil. Siqueira-Castro et al. (2009) found it there in primary settling tanks. However, it was also present "in fresh samples in natura, coexisting with *Paramecium aurelia* and testate amoeba (Siqueira-Castro et al. 2009, p. 775, Material and methods section). No further records published.

Deviata spirostoma (Alekperov, 1988) comb. nov.
(Fig. 101a, b, Table 31a)

1988 ***Kahliella spirostoma* Alekperov, sp. n.** – Alekperov, Zool. Zh., 67: 777, Fig. 1A, B (Fig. 101a, b; original description[1]; no formal diagnosis provided; the holotype slide [accession number: DB-14] and the paratype slide [DB-12] have been deposited in the Institute of Zoology of the National Academy of Science of Azerbaijan).

2001 ***Kahliella spirostoma* Alekperov, 1988** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 41 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2005 ***Kahliella spirostoma* Alekperov, 1988** – Alekperov, Atlas free-living infusoria, p. 217, Fig. $68_{5, 6}$ (Fig. 101a, b; guide to ciliates mainly described from Azerbaijan).

Nomenclature: No explicit derivation of the species-group name is given in the original description. The name *spirostom·us*, *-a*, *-um* ([m, f, n]; having a spiral-shaped mouth/adoral zone) is a composite of *he speira* (Greek noun; circular coil; Hentschel & Wagner 1996) and *to stóma* (Greek noun; mouth) and refers to the winding adoral zone of membranelles.

Remarks: Parental cirral rows and a gonostomatid oral apparatus – important features of *Kahliella* – are obviously lacking in the present species, indicating that it is misplaced in this genus. The slender habitus, the general cirral pattern, and the nuclear apparatus indicate that *K. spirostoma* belongs to *Deviata* to which it is therefore transferred. A transfer to *Deviata* is also discussed by Küppers & Claps (2010, p. 282). It differs from all other *Deviata* species, except for *D. polycirrata*, by the high number of adoral membranelles, namely 45–50 against 17–30 on average in the other species (Tables 31, 31a; key). *Deviata polycirrata* has more than twice as much cirral rows and short dorsal bristles (2 µm vs. 8–12 µm). Detailed redescription (live observation; illustration of exact cirral and kinety pattern of protargol-impregnated specimens; morphometry) strongly recommended, preferential from a population collected in the type locality area, the Caucasian region.

Morphology: Body length in life about 180 µm, 140–160 µm after wet silver nitrate impregnation; length:width ratio of specimen illustrated about 5:1 (Fig. 101a). Body slightly flattened dorsoventrally and contractile. Four macronuclear nodules, each with one micronucleus (Fig. 101b). Contractile vacuole near left cell margin behind adoral zone of membranelles. Presence/absence of cortical granules not checked. Movement very fast.

Adoral zone spiral-shaped, occupies about 25% of body length in specimen illustrated (Fig. 101a), composed of 45–50 membranelles; further details (e.g., shape and length of undulating membranes) not known. Buccal area/cavity obviously rather narrow according to Fig. 101a.

Cirral pattern as shown in Fig. 101a, that is, three enlarged frontal cirri, three cirral rows right of midline, two left marginal rows behind adoral zone of membranelles, and three cirral rows on dorsal side. Row behind right frontal cirrus composed of 30

[1] Since the original description is in Russian, I contacted Ilham Alekperov to inform me about the main features of this species.

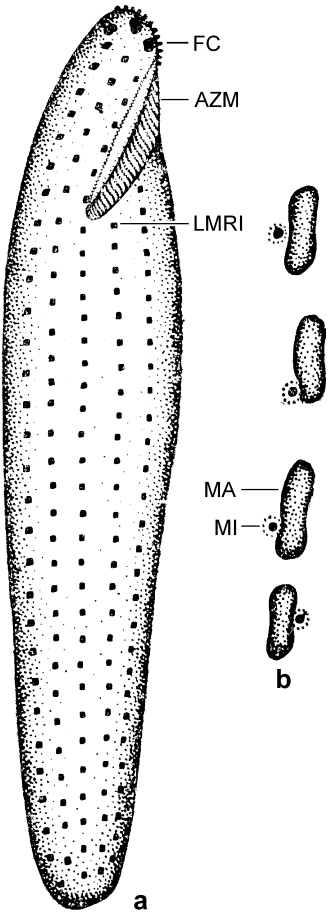


Fig. 101a, b *Deviata spirostoma* (from Alekperov 1988. a, wet silver nitrate impregnation; b, Feulgen stain). Infraciliature of ventral side and nuclear apparatus, a = 145 µm. AZM = adoral zone of membranelles, FC = left frontal cirrus (= cirrus I/1), LMRI = innermost left marginal row (= left marginal row 1), MA = macronuclear nodule, MI = micronucleus. Page 597.

cirri. Short and medium-length frontoventral row as well as transverse cirri lacking. Further details about cirral pattern (e.g., exact pattern on frontal area, buccal cirrus present or not, short frontoventral rows present or not) not described.

Dorsal bristles 8–12 µm long, arranged in two bipolar kineties and one which terminates at 50% of body length in left body portion. Exact arrangement not known. Caudal cirri lacking.

Occurrence and ecology: Type locality of *Deviata spirostoma* is a freshwater habitat about 20 km away from Ordubad City, South-West Azerbaijan, where Alekperov (1988) found it under meso- and polysaprobic conditions among putrefying vegetation.

Deviata polycirrata Küppers & Claps, 2010

(Fig. 102a–g, Tables 31, 31a)

2010 ***Deviata polycirrata* n. sp.**[1] – Küppers & Claps, J. Euk. Microbiol., 57: 275, 282, Fig. 2–19, Table 1 (Fig. 102a–g; original description; one hapantotype slide [accession number MLP 63] with protargol-impregnated individuals is deposited in the Colección de Invertebrados from Museo de la Plata, Buenos Aires Province, Argentina, and one paratype slide [USNM1135042] is deposited in the Ciliate Type slide Collection of the Smithsonian Institution, Washington, USA).

Nomenclature: The species-group name *polycirrat·us*, *-a*, *-um* (Latin adjective [m; f; n]; having many cirri) is a composite of the Greek indefinite quantifier *poly-* (many) and the Latin *cirratus* (curly-haired; cirrated in present case), and refers to the numerous rows of cirri (Küppers & Claps 2010, p. 283).

Remarks: *Deviata* species have a relatively uniform infraciliature. In spite of that, they can be distinguished by a combination of various features,

[1] Küppers & Claps (2010) provided the following diagnosis: Body size in vivo, 130–180 × 45–70 µm, with 8–9 long cirral rows on the right of the adoral zone of membranelles and 9–13 on the left of the latter, plus 3 long dorsal rows of dikinetids. Adoral zone with 39–48 membranelles. With four macronuclear nodules and one to two micronuclei. Single contractile vacuole located on the left body margin.

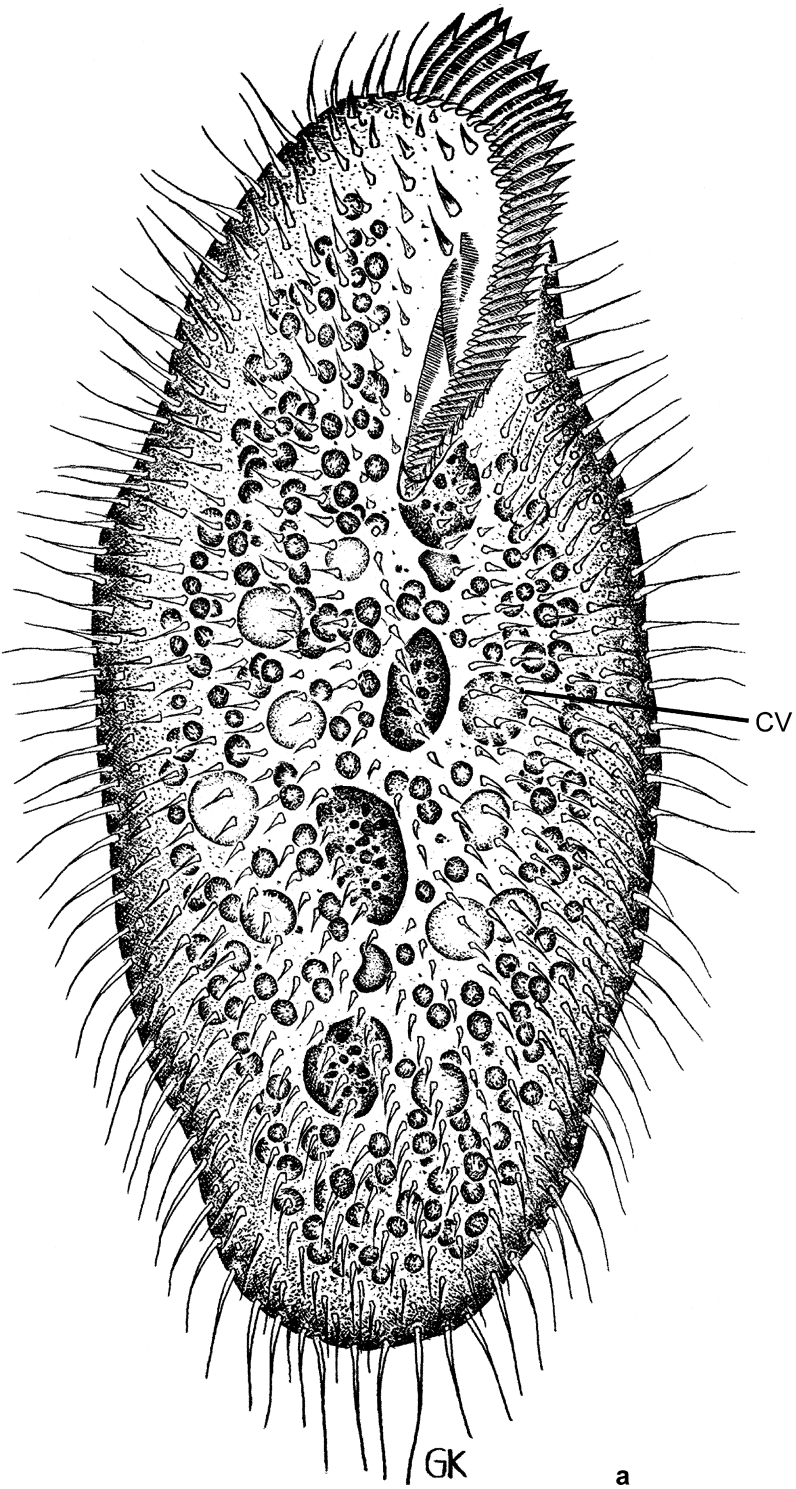
namely, the number of cirral rows, dorsal kineties, adoral membranelles, and macronuclear nodules (Tables 31, 31a). *Deviata polycirrata* can be clearly separated from three other quadrinucleate species (*D. bacilliformis*, *D. brasiliensis*, *D. quadrinucleata*), inter alia, by the higher number of dorsal kineties (3 vs. 1 or 2) and adoral membranelles (around 40 vs. around 20). *Deviata spirostoma*, which also has four macronuclear nodules and three dorsal kineties, can be distinguished from *D. polycirrata* in life by the length of the dorsal bristles (8–12 µm vs. 2 µm) and the lower number of cirral rows (5 on ventral side [Fig. 101a] vs. about 12 [Fig. 102b]). For separation from other *Deviata* species, see key and Table 31a.

Morphology: Body size 130–180 × 45–70 µm, on average 152 × 62 µm in life; by contrast, body very strongly inflated (181 × 130 µm on average) in protargol preparations made with the technique by Wilbert (1975); average length:width ratio about 2.5:1 in life and 1.4:1 in protargol preparations. Body outline variable, according to authors sometimes elliptical and slender with both ends rounded, sometimes globular with the anterior end pointed and flattened and the posterior rounded. Obviously these particulars refers to protargol-impregnated specimens (Fig. 102b), because according to the life data the outline is basically elliptical (Fig. 102a). Body very flexible. Invariably four macronuclear nodules arranged roughly along midline; individual nodules usually bilobed or ellipsoidal; two anterior and two posterior nodules connected by fine strand, which is sometimes faintly impregnated; chromatin bodies of usual size. Usually two micronuclei, each one often located between a pair of macronuclear nodules. Contractile vacuole about in mid-body, according to Fig. 102a distinctly set off from left body margin; collecting canals lacking. Defecation vacuole occasionally recognisable at rear end of cell. Cortical granules lacking. Cytoplasm colourless, but dark at low magnification (<10×) because of densely packed refractive granules (about 10 µm across) and ingested wheat starch from the culture.

Adoral zone occupies 30% of body length after protargol impregnation, composed on average of 43 membranelles of ordinary fine structure (Table 31), does not extend far posteriorly on right side of cell. Paroral and endoral composed of dikinetids, paroral commences at level of rearmost buccal cirrus in specimen illustrated (Fig. 102b), ends somewhat more anteriorly than endoral; both membranes usually only slightly curved and not or only inconspicuously optically intersecting (Fig. 14–19 in Küppers & Claps 2010); distinctly curved and intersecting in anterior portion of specimen illustrated (Fig. 102b). Buccal cavity small and flat. Pharyngeal fibres extend obliquely backwards.

Cirral pattern as in other *Deviata* species, except that number of cirral rows is rather high (Tables 31, 31a). Three enlarged frontal cirri close to distal end of adoral zone. Behind middle frontal cirrus invariably three buccal cirri[1] with rearmost one right of distal end of paroral. Parabuccal row (cirri behind right frontal cirrus) composed of 6–11 cirri, terminates slightly ahead level of buccal vertex (Fig. 102b). Further there are 17–21 cirral rows left and right of midline, many of them extend onto

[1] Küppers & Claps (2010) designate only the rearmost cirrus as buccal cirrus.



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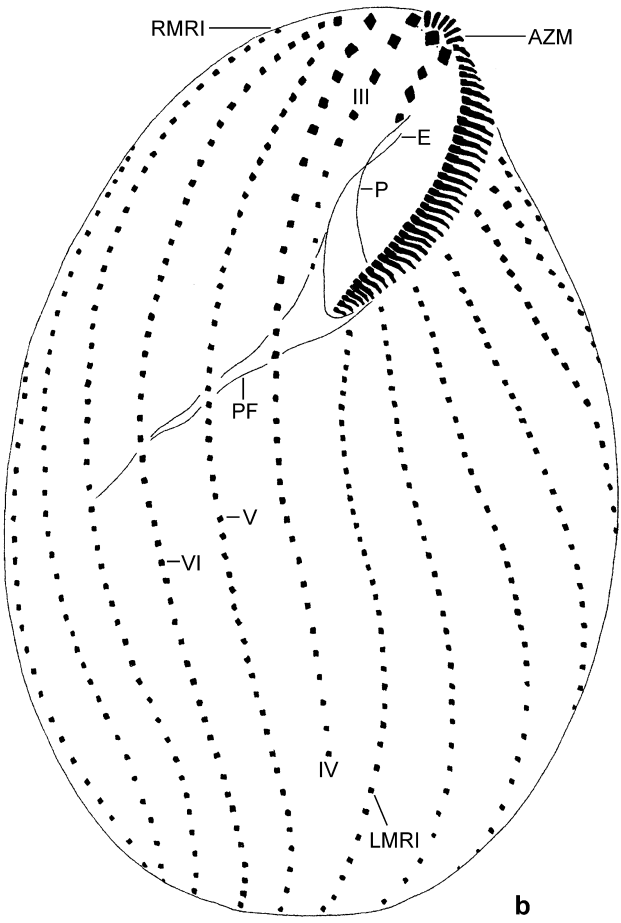

Fig. 102b *Deviata polycirrata* (from Küppers & Claps 2010. Protargol impregnation). Infraciliature of ventral side, 157 µm; dorsal side see (c). AZM = adoral zone of membranelles, E = endoral, LMRI = innermost left marginal row (= left marginal row 1; = L1 in original description), P = paroral, PF = pharyngeal fibres, RMRI = innermost right marginal row (R7 in original description), III = parabuccal row (R3 in original description), III–VI = frontal and frontoventral rows (R3 to R6 in original description). Page 598.

lateral and dorsal side. Right of parabuccal row eight or nine rows; all rows (except IV) roughly bipolar. Row IV often terminating in posterior third of cell, barely only slightly shortened posteriorly, and in 10 of 57 specimens observed it is not shortened posteriorly. Row V slightly shortened anteriorly. Left of midline 9–13 marginal rows commencing along left margin of adoral zone of membranelles; anterior cirri of each row composed of nine, six, or four basal bodies/cilia; remaining cirri made of four or two basal bodies only. Transverse cirri absent. Cirral rows usually more or less longitudinally arranged; slightly spiralling in impregnated specimens. Parental cirral rows lacking.

Variability of cirral pattern: In one specimen row IV is not extending beyond buccal vertex (Fig. 19 in Küppers & Claps 2010). One specimen with an additional

← **Fig. 102a** *Deviata polycirrata* (from Küppers & Claps 2010. From life). Ventral view, size not indicated. CV = contractile vacuole. Page 598.

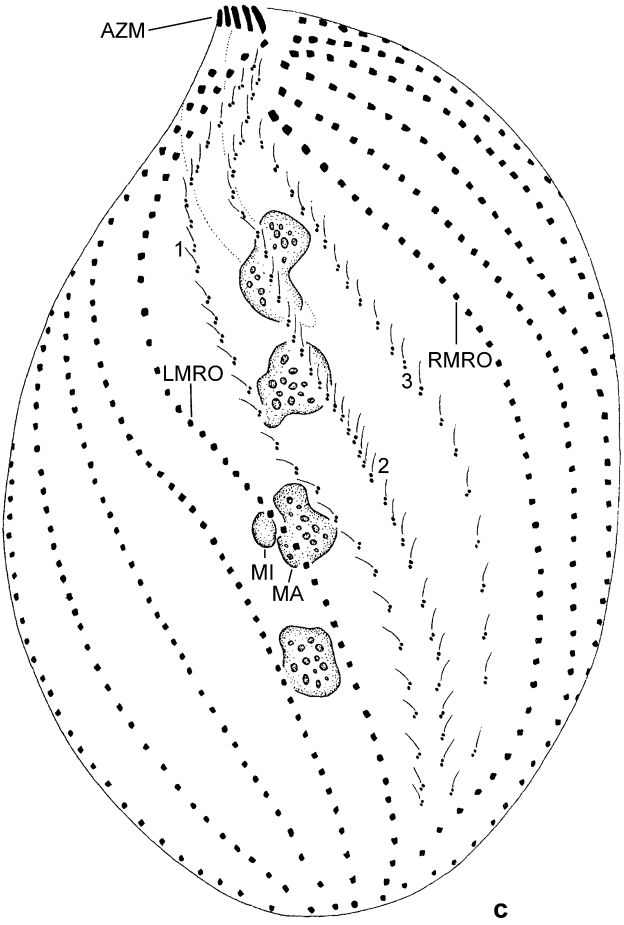

Fig. 102c *Deviata polycirrata* (from Küppers & Claps 2010. Protargol impregnation). Infraciliature of dorsal side, 157 µm; ventral side see (b). AZM = adoral zone of membranelles, LMRO = outermost left marginal row (L9 in original description), MA = macronuclear nodule, MI = micronucleus, RMRO = outermost right marginal row (R12 in original description), 1–3 = dorsal kineties. Page 598.

short row of five narrowly spaced cirri between parabuccal row and row IV. A further specimen also with this additional row composed of 13 cirri, row IV terminates subequatorially, and a further short extra row of nine cirri behind buccal vertex. One specimen with parabuccal row extending beyond buccal vertex while row IV terminates in cell centre.

Invariably three dorsal kineties in and close to midline of dorsal side. Bristles of kinety 2 more closely spaced than those in remaining rows; sometimes kinety 2 extends more posteriorly than rows 1 and 3. Kinety 3 somewhat shorter anteriorly. According to Küppers & Claps (2010, p. 276), kinety 3 is one or two bristles shorter; however, according to Fig. 102c the difference is obviously up to three basal body pairs (Table 31). Dorsal bristles about 2 µm long in life (Table 31). Caudal cirri lacking.

Cell division (Fig. 102d–g). Küppers & Claps (2010) found only two well-impregnated dividers. Thus, the exact origin of the anlagen I–VI remains ambiguous

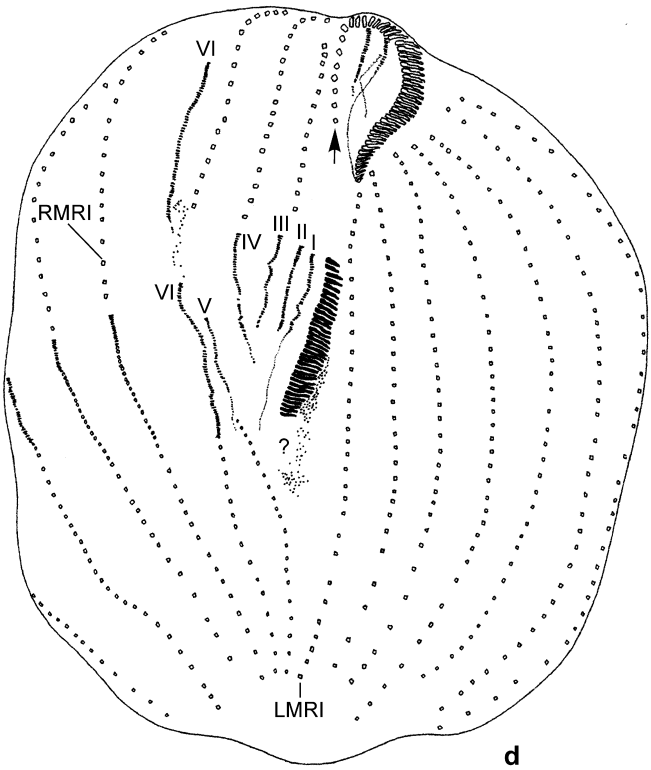

Fig. 102d *Deviata polycirrata* (from Küppers & Claps 2010. Protargol impregnation). Infraciliature of ventral side of middle divider, 215 µm; dorsal side, see (e). Arrow marks rear end of parental parabuccal row. LMRI = innermost left marginal row (= left marginal row 1; = L1 in original description), RMRI = innermost right marginal row (R7 in original description), I–VI = frontal and frontoventral rows, ? = dark impregnated area. Page 598.

and details should not be overinterpreted, inasmuch as the morphogenesis of this type of hypotrichs is difficult to follow, even when more states are available.

In the middle divider the anterior portion of the adoral zone of the opisthe is well differentiated (Fig. 102d). The anlagen I–IV of the opisthe are already rather long and probably originate from the oral primordium. The middle portion of parental row VI (R6 in original description) has, very likely, formed a long primary primordium, which has split into an anterior portion right of the parental row VI and a posterior portion, which has replaced the parental row VI. Anlage VI of the opisthe lengthens posteriad by modification of the parental row. A slender field of loosely spaced basal bodies remains between the two anlagen. According to Küppers & Claps (2010), anlage V of the opisthe apparently also forms from the disaggregating cirri ("slender field" mentioned above) of the parental row VI, migrates posteriad and connects with parental row V. Simultaneously, the anterior portion of parental row VI remains unchanged. The parental undulating membranes dedifferentiate. As is usual, frontal cirrus I/1 is formed from the undulating membrane anlage while anlage II originates from the buccal row. In the right marginal rows (from R7 towards right) intrakinetal anlagen develop about in mid-body. The left marginal rows remain unchanged. Dorsal kinety anlagen originate at two levels within rows 1 and 2

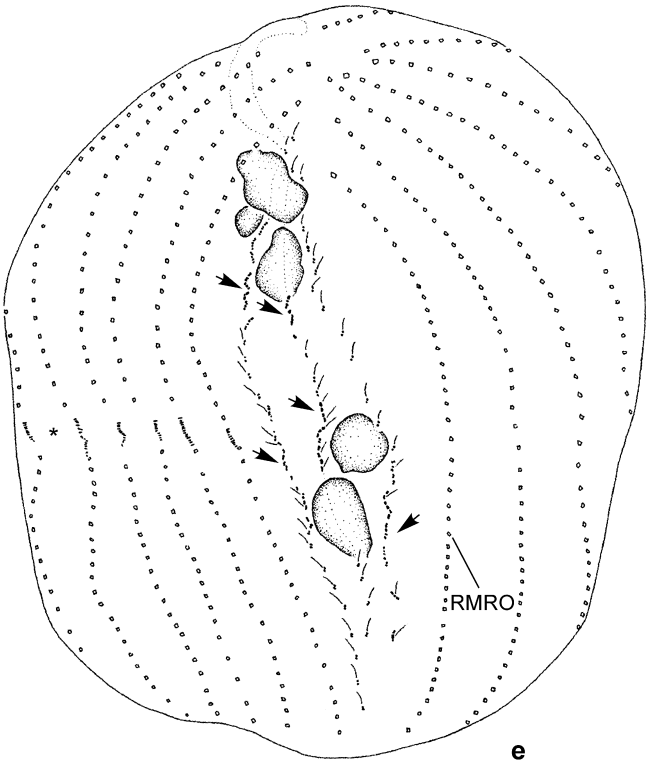

Fig. 102e *Deviata polycirrata* (from Küppers & Claps 2010. Protargol impregnation). Infraciliature of dorsal side and nuclear apparatus of middle divider, 215 µm; ventral side see (d). Arrows mark dorsal kinety primordia. Asterisk marks level at which left marginal row primordia of the opisthe occur. RMRO = outermost right marginal row. Page 598.

and at a rear level in kinety 3 (Fig. 102e). At that stage parental dikinetids remain among the anlagen. The macronuclear nodules are not yet fused.

In the late divider found by Küppers & Claps (2010) the four macronuclear nodules are fused to a single ellipsoidal mass (Fig. 102f, g). Anlage VI of the proter obviously fuses with the anterior portion of parental row VI. Perhaps, proter's anlage V developed within the anterior part of the parental row while anlage IV of the proter could have developed within parental row V. As aforementioned, the data are too sparse and the process too complex to elucidate the exact origin of the anlagen IV–VI in proter and opisthe. Thus, the data are not included in Table 31b. The anlagen I–III, are obviously formed, as is usual, from parental structures in the proter, and the oral primordium in the opisthe. Distinctly more very well impregnated dividers are needed to ascertain the exact process of cell division in *D. polycirrata*. The left marginal rows are formed in the ordinary manner, that is, within each parental row two anlagen occur. Very likely, no parental cirri are retained after division. Dorsomarginal kineties and caudal cirri are not formed.

The formation of the primary primordia in row VI strongly indicates that the classification in *Deviata* is correct, but as just mentioned more detailed data about the ontogenesis are needed for a serious comparative analysis.

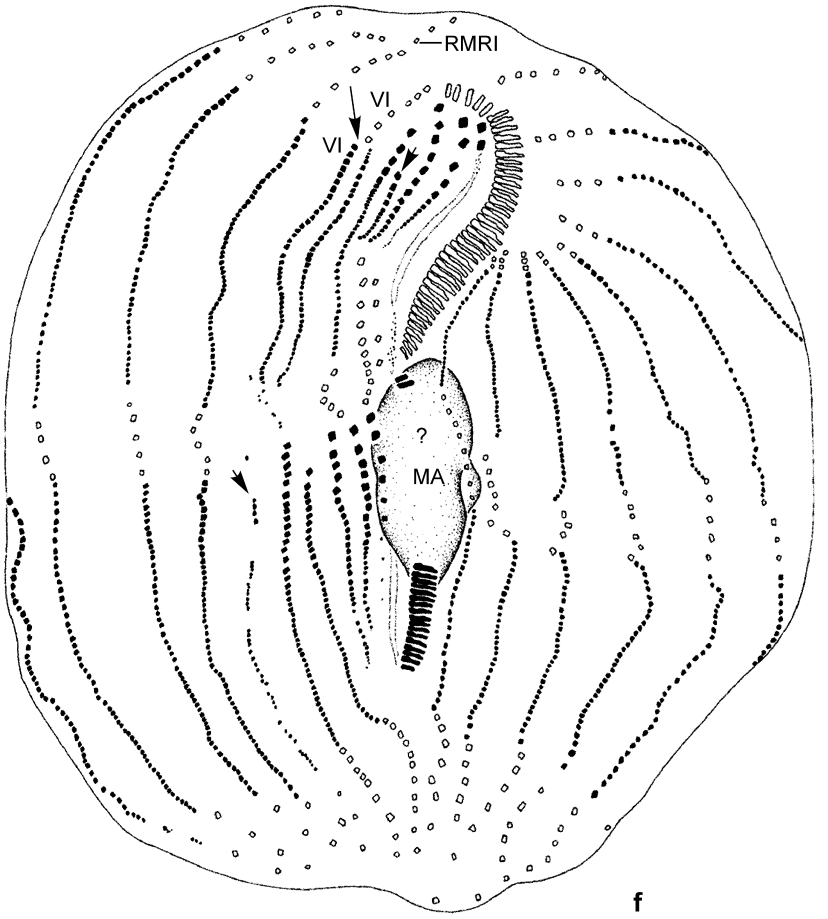

Fig. 102f *Deviata polycirrata* (from Küppers & Claps 2010. Protargol impregnation). Infraciliature of ventral side of late divider, 193 µm; dorsal side see (g). Short arrows mark additional cirral rows. Long arrow marks site where the anterior portion of the parental row VI fuses with anlage VI of proter. Parental cirri white, new black. MA = fused macronucleus, RMRI = innermost right marginal row, VI = parental frontoventral row and anlage VI of proter, ? = dark impregnated area. Page 598.

Occurrence and ecology: So far *Deviata polycirrata* is only recorded from the type locality, that is, a temporary pond about 18 km east of Dolores city near the Provincial Route No. 63 (36°18'55"S 57°32'12"W), Buenos Aires Province, Argentina. According to Küppers & Claps (2010), the pond was covered by the floating macrophytes *Lemna* sp., *Spirodella* sp., and *Limnobioum spongiae*. The following physicochemical parameters were measured: pH 7; electrical conductivity 242 µS cm^{-1}; water temperature 15.5 °C; total dissolved solids 0.16 g l^{-1}; water depth 40–55 cm. Water samples were collected during February 2004.

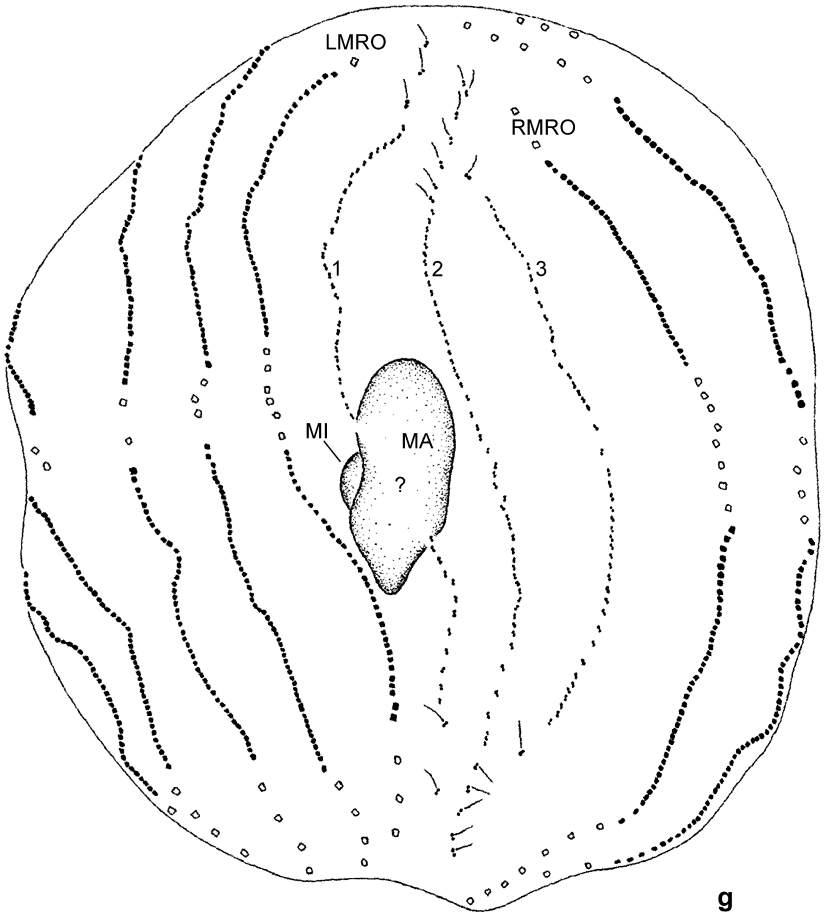

Fig. 102g *Deviata polycirrata* (from Küppers & Claps 2010. Protargol impregnation). Infraciliature of dorsal side and nuclear apparatus of late divider, 193 µm; ventral side see (f). Parental cirri white, new black. LMRO = outermost left marginal row, MA = fused macronucleus, MI = micronucleus, RMRO = outermost right marginal row, 1–3 = dorsal kineties, ? = dark impregnated area. Page 598.

Deviata rositae Küppers, Lopretto & Claps, 2007
(Fig. 103a–d, Tables 31, 31a)

2007 ***Deviata rositae* n. sp.**[1] – Küppers, Lopretto & Claps, J. Euk. Microbiol., 54: 443, 446, Fig. 1–7, Table 1 (Fig. 103a–d; original description; the holotype slide [accession number: MLP029] is depos-

[1] Küppers et al. (2007) provided the following diagnosis: Size in vivo 112–154 × 21–28 µm. Contractile vacuole without collecting canals, in mid-body on the left. Macronucleus moniliform, with 7–14 nodules. With 1–3 micronuclei. Adoral zone with 14–18 membranelles. With four frontal cirri, one buccal cirrus, six long and slightly spiralled rows of cirri, and two dorsal rows of dikinetids. Right-most dorsal kinety composed of few dikinetids, at the anterior end of the body.

ited in the Coleccíon de Invertebrados of the Museo La Plata, La Plata, Buenos Aires Province, Argentina; a paratype slide [USNM11106151] is deposited in the Ciliate Type Slide Collection, Smithsonian Institution, Washington, USA).

Nomenclature: The authors dedicated this species to Rosa E. Pettigrosso (nickname "Rosita"), a pioneer in the study of ciliates in Argentina.

Remarks: This species was assigned to *Deviata* on the bases of Eigner's (1995) characterisation, that is, the increased number of cirral rows and the lack of parental cirri (Küppers et al. 2007). However, ontogenetic data are lacking so that the origin of the various rows is not known and a correct designation therefore not possible. I suppose that *D. rositae* has one right marginal row and two long frontoventral rows. This would mean that the frontoventral ciliature originates from five anlagen (Fig. 103b, d).

Deviata rositae differs from the other *Deviata* species, inter alia, in the number of macronuclear nodules, namely 7–14 against two or 2–4 (Tables 31, 31a). *Deviata bacilliformis*, which has relatively often four nodules, has only one dorsal kinety whereas one long and one short kinety is present in *D. rositae*; however, they agree in having somatic cirri composed of two basal bodies only. *Deviata estevesi*, which was discovered also in South America, has usually two macronuclear nodules and the contractile vacuole in the body centre (Fig. 104a–n). In addition, the three frontal cirri are more pronounced in *D. rositae* than in *D. estevesi*. Thus, the species status of *D. rositae* is beyond reasonable doubt. For separation from other *Deviata* species, see key and Table 31a.

The posterior part of dorsal kinety 1 is somewhat separated from the main portion of the kinety (Fig. 103c). A similar situation is described in *D. estevesi* (Fig. 104l), where these separated bristles are the rear portion of kinety 2. Ontogenetic data on *D. rositae* are needed to decide whether or not the patterns are homologous.

Morphology: Body size in life about 112–154 × 21–28 µm. Body vermiform, that is, longish and round in cross-section; anterior portion, however, slightly dorsoventrally flattened; very flexible. Macronucleus moniliform, that is, composed of 7–14 spherical, ellipsoidal, or fusiform nodules connected via a fine strand. 1–3 ellipsoidal micronuclei; usually one near the anteriormost macronuclear nodule, the others near the posterior nodules (Fig. 103b, c). Contractile vacuole without collecting canals, in mid-body close to left cell margin, empties dorsally (Fig. 103a). Some specimens with a large defecation vacuole in rear cell end. Cortical granules lacking. Cytoplasm colourless with refractive granules 6–8 µm across making cells greyish to blackish at low (<40×) magnification; food vacuoles with 12–18 µm-sized, refractive structure, possibly wheat starch. Swims in spirals, but immobile when feeding on the substrate.

Oral apparatus inconspicuous because adoral zone occupies only 21% of body length on average, composed of 14–18 membranelles of usual fine structure, that is, made of four rows of basal bodies (Table 31); distal end of zone almost not extending onto right body margin. Endoral somewhat longer than paroral, extends from proximal end of adoral zone to buccal cirrus. Paroral slightly overlapping with ante-

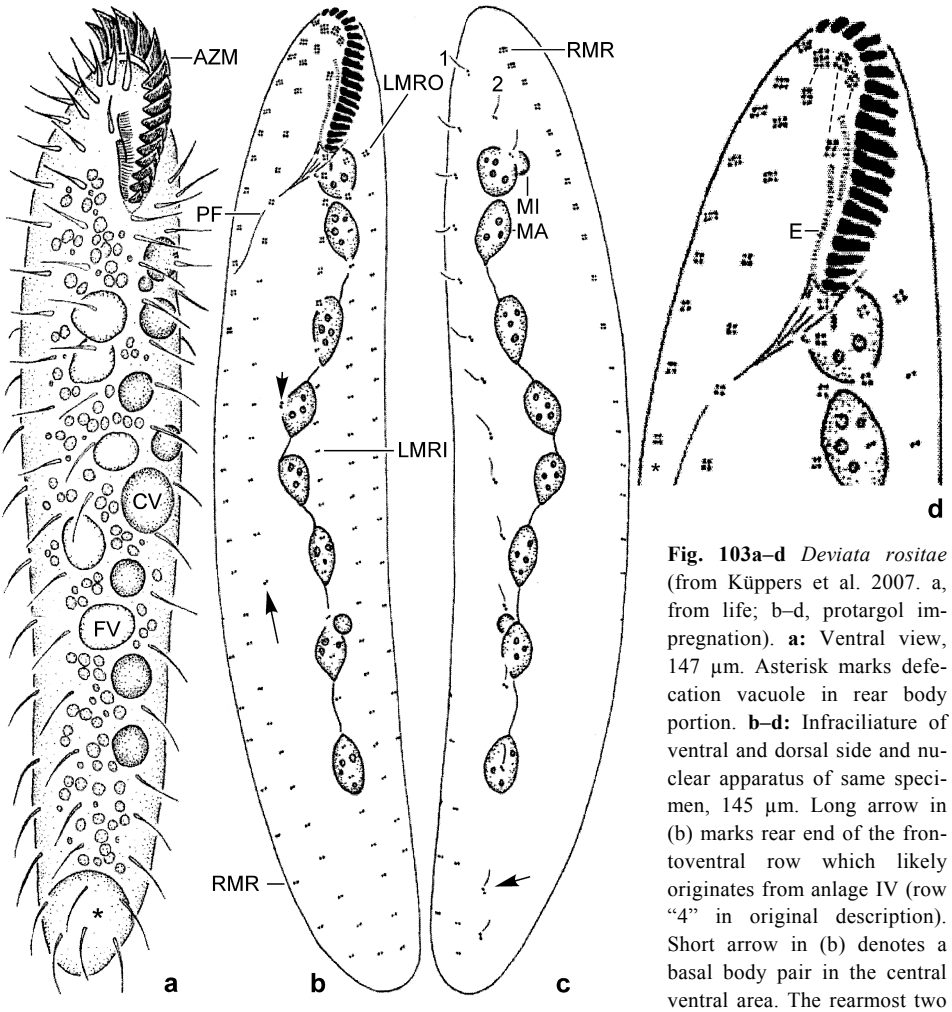

Fig. 103a–d *Deviata rositae* (from Küppers et al. 2007. a, from life; b–d, protargol impregnation). **a:** Ventral view, 147 µm. Asterisk marks defecation vacuole in rear body portion. **b–d:** Infraciliature of ventral and dorsal side and nuclear apparatus of same specimen, 145 µm. Long arrow in (b) marks rear end of the frontoventral row which likely originates from anlage IV (row "4" in original description). Short arrow in (b) denotes a basal body pair in the central ventral area. The rearmost two bristles of dorsal kinety 1 (arrow in c) are somewhat separated from the main portion of this kinety. Broken lines in (d) connect cirri/structures originating from same anlage (only shown for anlagen I–III); frontal cirri connected by dotted line. Asterisk in (d) marks right frontoventral row (row "5" in original description). AZM = adoral zone of membranelles, CV = contractile vacuole, E = endoral, FV = food vacuole, LMRI, LMRO = inner (= left marginal row 1; = row "3" in original description) and outer (row "1" in original description) left marginal row, MA = macronuclear nodule, MI = micronucleus, PF = pharyngeal fibres, RMR = right marginal row (row "6" in original description), 1, 2 = dorsal kineties 1 and 2. Page 606.

rior portion of endoral and extending somewhat ahead of level of buccal cirrus; both membranes more or less straight and composed of dikinetids, do not intersect optically (Fig. 103b, d). Pharyngeal fibres extend obliquely to right cell margin.

Cirral pattern of usual variability (Table 31). Cirri usually composed of two basal bodies only, except for those in the anterior body portion. Frontal cirri slightly en-

larged, that is, composed of nine basal bodies each and very narrowly spaced. Buccal cirrus (six basal bodies) ahead of anterior end of endoral and right of paroral. Parabuccal cirrus (= cirrus III/2) behind right frontal cirrus, also composed of six basal bodies. Invariably (n = 20) six cirral rows. Left frontoventral row (row IV?) composed of 14 cirri on average, commences right and slightly behind parabuccal cirrus (= cirrus III/2) and terminates slightly ahead of or behind mid-body; in specimen illustrated it ends at 59% of body length (Fig. 103b, long arrow). Anterior end of right frontoventral row (row V or VI?) close to distal end of adoral zone, extends to near rear cell end. Size of cirri decreases from six over four to two cilia in posteriad direction in three rightmost rows.[1] Usually one pair of non-ciliated basal bodies (rarely two pairs or three closely spaced basal bodies) left of middle portion of left frontoventral row (Fig. 103b, short arrow). Transverse cirri lacking. Right marginal row (= cirral row 6 in original description) begins dorsolaterally and terminates ventrally about at same level as right frontoventral row. Three left marginal cirral rows with anteriormost cirri composed of four basal bodies; inner row commences close to rear end of adoral zone, terminates usually on ventral, rarely on dorsolateral side of rear body end; middle and outer row begin about at same level, but extend onto dorsolateral side posteriorly.

Dorsal bristles about 3.5 µm long on average, arranged in two kineties of very different length (Fig. 103c, Table 31). Kinety 1 commences near anterior body end and extends slightly sigmoidally to near rear cell end; rearmost two dikinetids somewhat separated from anterior portion (whether or not this is the same pattern as in *D. estevesi* has to be checked by ontogenetic data; see remarks). Kinety 2 composed of two bristles only; commences at 11% of body length in specimen illustrated (Fig. 103c). Caudal cirri lacking.

Occurrence and ecology: Semiterrestrial; possibly confined to South America. Type locality of *Deviata rositae* is a temporary freshwater pond (35°05'S 57°48'W) about 40 km south of the city of La Plata, Buenos Aires province, Argentina; Küppers et al. (2007) collected the sample during the dry phase (January 2005), that is, *Deviata rositae* can make cysts. Dry periods are mainly during summer. The sample contained the uppermost layer (5 cm) of dry sediment as well as dead macrophytes. *Deviata rositae* feeds on bacteria, but likely also on wheat starch (Küppers et al. 2007).

Incertae sedis in *Deviata*

Deviata estevesi Paiva & Silva-Neto, 2005
(Fig. 104a–y, Tables 31, 31a)

2005 ***Deviata estevesi* sp. n.**[2] – Paiva & Silva-Neto, Acta Protozool., 44: 352, Fig. 3–32, Table 1 (Fig. 104a–q; original description; the slides containing the holotype [accession number: IBZ-UFRJ

[1] Anteriormost cirri of right marginal row composed of four basal bodies according to text of original description; however, Fig. 103c clearly shows that the anteriormost two cirri are made of six basal bodies each.

[2] Paiva & Silva-Neto (2005) provided the following diagnosis: Size in vivo about: 100 × 40 µm (n = 15).

0008-6-1] and paratypes [IBZ-UFRJ 0008-7-1] are deposited in the collection of the Laboratório de Protistologia, Dept. de Zoologia, Inst. de Biologia–CCC, Universidade Federal do Rio de Janeiro [UFRJ]).

2009 ***Parastrongylidium estevesi* (Paiva & Silva-Neto, 2005) comb. nov.** – Siqueira-Castro, Paiva & Silva-Neto, Zoologia, 26: 775, Fig. 1–20, Table 1 (Fig. 104r–y; redescription and combination with *Parastrongylidium*. One voucher slide [accession number IBZ 0007-2] is deposited in the collection of the Laboratório de Protistologia of the UFRJ).

Nomenclature: Paiva & Silva-Neto (2005) dedicated the species to Francisco de Assis Esteves.

Remarks: *Deviata estevesi* differs from the congeners by the frontal ciliature because it has distinctly more buccal cirri and parabuccal cirri forming two cirral rows ahead the undulating membranes (Fig. 104k, n). Further, the three frontal cirri are difficult to recognise because they are not (distinctly) larger than the remaining cirri. Paiva & Silva-Neto (2005) postulated that a buccal cirrus is lacking. By contrast, I suppose that the specimen shown in Fig. 104k, n has four buccal cirri and six parabuccal cirri. The row which terminates about in mid-body is likely the row formed by anlage IV. The second cirrus from anterior in row "R1" (Fig. 104k) is likely the leftmost frontal cirrus formed by anlage I (Fig. 104n), and the anteriormost cirrus of this row is the middle frontal cirrus and the remaining cirri form the buccal row. If my assumption is correct, then *D. estevesi* has – like the type species – obviously constantly six frontoventral cirri anlagen/rows. However, when the interpretation made in the original description is confirmed, then the classification in the present genus is uncertain.

I wrote the previous paragraph before the paper by Siqueira-Castro et al. (2009) was published. These authors studied a second population of *Deviata estevesi*, including some ontogenetic stages (Fig. 104r–y). Unfortunately, the results concerning the origin of row "R1" are not very convincing so that the transfer to *Parastrongylidium* proposed by Siqueira-Castro et al. (2009) is uncertain. In the following paragraphs the pros and cons for the preservation of the original generic assignment are discussed, based on the results by Fleury & Fryd-Versavel (1984; *P. martini*), Aescht & Foissner (1992; *P. oswaldi*), Eigner (1995; *D. abbrevescens*), Salvadó & Fernández-Galiano (1997; *P. oswaldi*), Paiva & Silva-Neto (2005; *D. estevesi*), and Siqueira-Castro et al. (2009; *D. estevesi*).

The following features indicate that the present species belongs to *Deviata*:

Short frontoventral rows. The present species has – like *Deviata abbrevescens* (type of *Deviata*) – three short (i.e., non-bipolar) frontoventral rows, designated as

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Dark, or almost black coloration under dissection microscope. Cortical granules lacking. Cytoplasm filled with compact crystals measuring about 3–5 µm. Body flexible and contractile, with outline variable, but usually narrowed at the anterior end and broad at the posterior end. Dorsoventrally flattened in the anterior region and ellipsoid in cross section below the cell equator. With small, round contractile vacuole located at the mid-body, away from its margins. Cirri arranged in 7 rows right of adoral zone of membranelles and 4 rows left of it. Row R1 with 5–7 cirri; R2 with 6–9 cirri; R3 always ending in equatorial region of body. Buccal cirrus absent. Nuclear apparatus composed of usually two macronuclear nodules and two micronuclei. Two dorsal kineties, right kinety posterior shortened. A short file of dorsal cilia, possible an extension of the right kinety, is present at the posterior region of body.

rows II–IV according to my terminology (Fig. 96g, 104m, n). By contrast, *Parastrongylidium* species lack such short rows (Fleury & Fryd-Versavel 1984, Aescht & Foissner 1992) or has sometimes only one very short row (Salvadó & Fernández-Galiano 1997).

Dorsal kineties. *Deviata estevesi* has two dorsal kineties. Kinety 1 is bipolar, kinety 2 consists of a moderate long anterior portion and a short posterior portion (Fig. 104l, q, s). Parental structures are not retained. The type species *D. abbrevescens* also has two dorsal kineties; kinety 1 is bipolar, kinety 2 has widely spaced bristles, especially in the posterior portion (Fig. 96h). By contrast, both *Parastrongylidium* species have a single dorsal kinety. Aescht & Foissner (1992, p. 228) occasionally found a second, short kinety in the posterior body half; probably a residue from the parental generation.

Macronucleus. Basically all species so far assigned to *Deviata* have two or more distinct macronuclear nodules, although the nodules of some (all?) species are connected by a more or less fine thread (e.g., Fig. 96a, b, h, 100b, 103b, 104b). *Parastrongylidium* spp. have a single moniliform or rather irregular macronucleus. Salvadó & Fernández-Galiano (1997) also found in most cases such a macronucleus, but they also isolated few specimens with 1–10, uneven nodules.

Replication band. *Deviata estevesi* forms – like *D. abbrevescens* – replication bands during early stages of cell division (Fig. 96k, 104p; Fig. 23 in Paiva & Silva-Neto 2005). By contrast, both *Parastrongylidium martini* and *P. oswaldi* lack these structures (Fleury & Fryd-Versavel 1984, p. 532; Aescht & Foissner 1992, p. 228); Salvadó & Fernández-Galiano (1997, p. 183) are somewhat uncertain. Whether the ancestor of *Parastrongylidium* never had a replication or lost it is not known.

Frontoventral anlage II. In *D. estevesi* and *D. abbrevescens* anlage II of the opisthe originates from the oral primordium (Fig. 96k, l, 104u). In *P. oswaldi* this anlage is formed within the parental row (Fig. 19, 20 in Aescht & Foissner 1992). Unfortunately, the data by Fleury & Fryd-Versavel (1984) are not ambiguous in this respect.

The following feature indicates that *D. estevesi* belongs to *Parastrongylidium*:

Frontoventral anlagen III–VI. In *Parastrongylidium* the frontoventral rows III to VI are formed within the corresponding parental row (Fig. 19–21 in Aescht & Foissner 1992). The same obviously applies to *Deviata estevesi*, although the data are not very cogently (Fig. 104t, u, w).

The following features support neither the original assignment nor the transfer to *Parastrongylidium*:

Habitat. All species discussed were found in highly eutrophic and/or saprobic habitats. *Deviata estevesi*: brackish water and sediment from the bottom of a lagoon (Paiva & Silva-Neto 2005), raw sewage from primary settling tanks of a sewage treatment plant (Siqueira-Castro et al. 2009). *Deviata abbrevescens*: bottom of pond (Eigner 1995). *Parastrongylidium martini*: manure/dung (Fleury & Fryd-Versavel 1984). *Parastrongylidium oswaldi*: activated sludge of heavily loaded industrial sewage plant (Aescht & Foissner 1992), conventional activated sludge plants (Salvadó & Fernández-Galiano 1997).

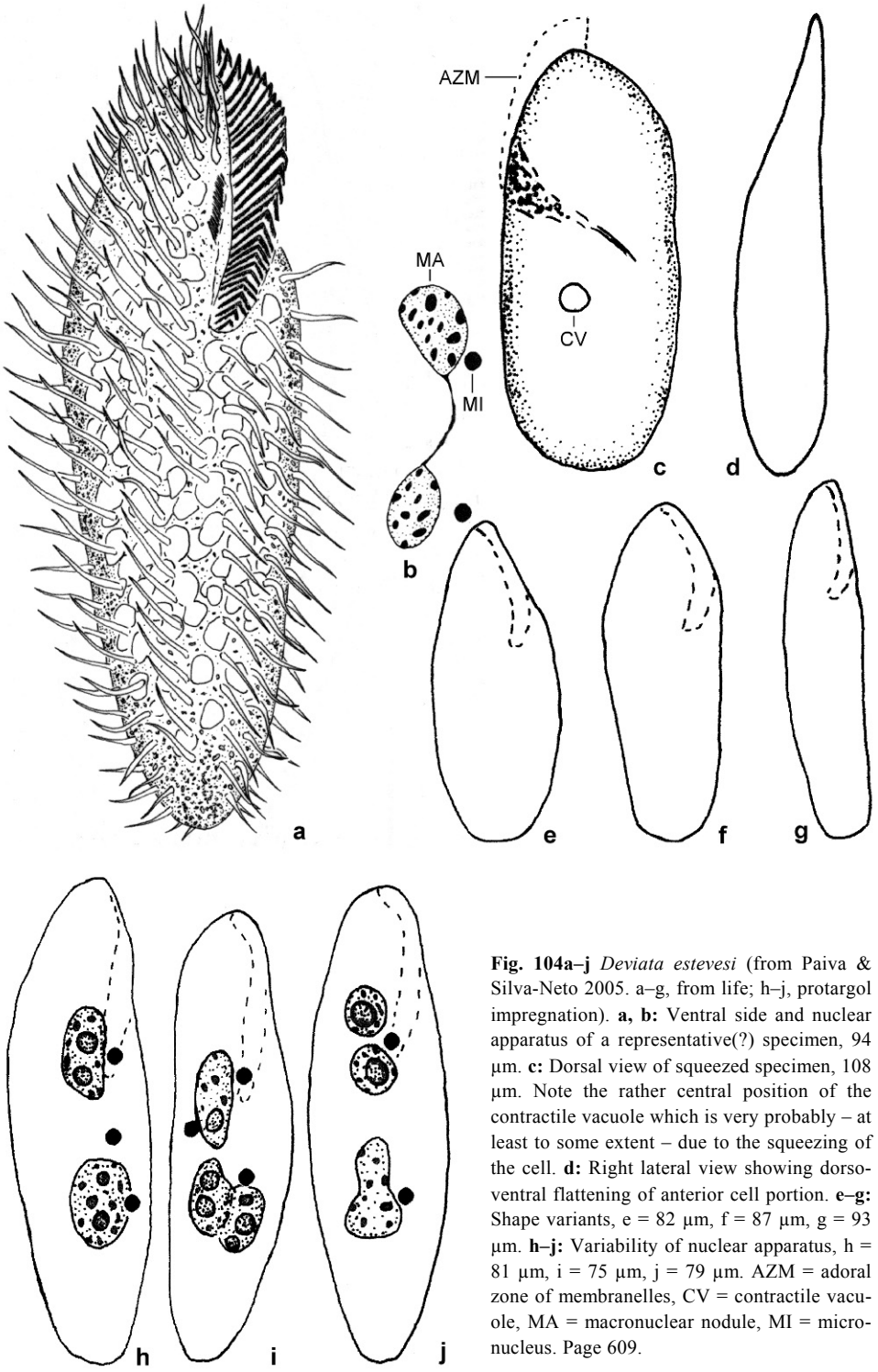


Fig. 104a–j *Deviata estevesi* (from Paiva & Silva-Neto 2005. a–g, from life; h–j, protargol impregnation). **a, b:** Ventral side and nuclear apparatus of a representative(?) specimen, 94 µm. **c:** Dorsal view of squeezed specimen, 108 µm. Note the rather central position of the contractile vacuole which is very probably – at least to some extent – due to the squeezing of the cell. **d:** Right lateral view showing dorsoventral flattening of anterior cell portion. **e–g:** Shape variants, e = 82 µm, f = 87 µm, g = 93 µm. **h–j:** Variability of nuclear apparatus, h = 81 µm, i = 75 µm, j = 79 µm. AZM = adoral zone of membranelles, CV = contractile vacuole, MA = macronuclear nodule, MI = micronucleus. Page 609.

Cortical granules. All *Deviata* species, including *D. estevesi*, and *P. martini* (see Aescht & Foissner 1992, p. 232) lack cortical granules. By contrast, *Parastrongylidium oswaldi* has such organelles (Aescht & Foissner 1992, Salvadó & Fernández-Galiano 1997).

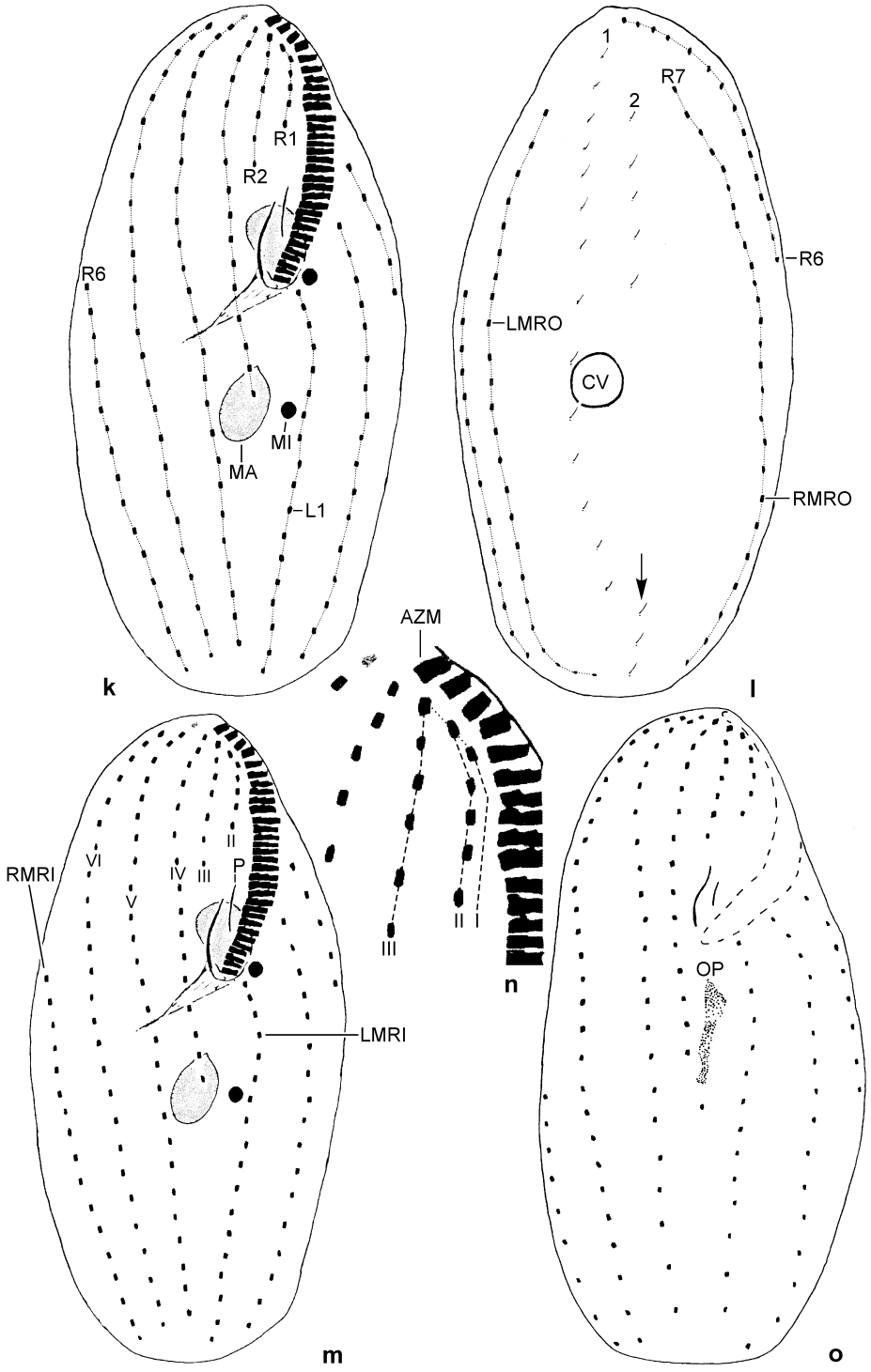
The previous analysis shows that *Deviata estevesi* cannot be assigned to *Deviata* or *Parastrongylidium* with certainty. Thus, its original generic assignment is preliminary retained. To document the tentativeness it is classified as incertae sedis. A detailed reinvestigation of the cell division and molecular data of *D. estevesi* and the two type species are likely needed for a better estimation of the phylogenetic position.

Morphology: The following characterisation is based on the original description (Paiva & Silva-Neto 2005). Since the population described by Siqueira-Castro et al. (2009) agrees very well with the type material, only additional or deviating data are summarised in a paragraph; more details, see Table 31 and Fig. 104r–y.

Body size in life about 100 × 40 µm (n = 15), that is, length:width ratio 2.5:1; on average 2:1 in protargol preparations (Table 31). Body outline elongate elliptical with anterior end usually narrowly and posterior end broadly rounded. Body flexible and contractile, dorsoventrally flattened in anterior portion and elliptical in cross section behind mid-body. Usually two ovoid macronuclear nodules about in cell midline, anterior nodule usually above proximal portion of adoral zone; in some specimens nodules connected by very thin isthmus, a structure not recognisable in other specimens likely because poorly stained (Fig. 104b). In specimens with few cytoplasmic crystals, macronuclear nodules more or less elliptical, sometimes irregular shaped, increased in size in relation to body dimension, or increased in number; in some individuals nodules narrowed equatorially or bisected; chromatin bodies 1–5 µm across, larger ones stain lighter than smaller ones (Fig. 104b, h–k). Usually each one micronucleus (about 3 µm across) close to macronuclear nodules. Contractile vacuole almost in cell centre near dorsal side, globular, and without collecting canals during diastole, which lasts about 10 s; systole lasts about 1 s (Fig. 104c). Overall appearance dark or almost black under dissecting microscope. Cortical granules lacking. Cytoplasm with numerous compact, 3–5 µm-sized, transparent, light-greenish crystals; do not stain with protargol, but remain visible in slides; often cause cell rupture during fixation; number of crystals decreases in specimens of old cultures, perhaps due to starvation; crystals separated from cell surface by an about 3 µm thick layer of smaller, irregular shaped cytoplasmic granules[1]. Usually swimming among sediment particles, rotating about main body axis; sometimes gliding on bottom of Petri dishes and crawling over sediment particles; very rarely, *D. estevesi* shows, in contrast to *D. abbrevescens*, highly thigmotactic behaviour.

Adoral zone rather prominent because occupying about 38% of body length on average in protargol preparations and composed of 28–33 membranelles (Table 31); commences at anterior end of cell, and therefore not formed like a question mark, but rather gonostomatid. Membranelles of middle portion about 5 µm wide. Undu-

[1] According to Fig. 18 in Paiva & Silva-Neto (2005) these structures look like mitochondria.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lating membranes inconspicuous, only slightly curved and not intersecting optically. Paroral commencing more anteriorly and somewhat shorter than endoral. Pharyngeal fibres extend obliquely rightwards (Fig. 104a, c, m).

Cirral pattern rather stable, number of cirri within rows of usual variability (Fig. 104k–n, p, q, Table 31). All cirri 8–12 µm long and very thin because composed of four cilia only. Exact designation of cirri and rows not yet possible, because for reasons explained in the remarks. Frontal ciliature somewhat unusual because frontal cirri not (distinctly) enlarged. Leftmost cirral row (buccal row?) somewhat shorter than next (parabuccal?) row; both rows terminate more or less distinctly ahead of undulating membranes. Next row perhaps homologous with row formed from anlage IV in *D. abbrevescens*, because terminating in cell centre in both species. Rows right to this row of body length, outermost two rows (marginal rows?) extend dorsolaterally anteriorly. Invariably four left marginal rows, inner one commences at proximal end of adoral zone, outermost begins at 15% of body length in specimen illustrated (Fig. 104k–n). All cirral rows terminating near body end not distinctly curved posteriorly, except for the outermost left marginal row. One out of 25 specimens investigated with one postoral (termed postperistomial in original description) ventral cirrus (Fig. 104p). Pretransverse ventral cirri and transverse cirri lacking.

Length of dorsal cilia not mentioned in original description, according to a photomicrograph (Fig. 32 in Paiva & Silva-Neto 2005) about 2–3 µm. Dikinetids arranged in two rows. Kinety 1 commences anteriorly, ends subterminal. Usually three bristles (mean = 3.4, range = 3–5, SD = 0.9; n = 5) form a short row somewhat right of rear end of kinety 1 (Fig. 104l, q); according to the ontogenetic data by Siqueira-Castro et al. (2009), this is the posteriorly displaced rear portion of kinety 2, which extends from 16% to 41% of body length in specimen illustrated (Fig. 104l). Caudal cirri lacking.

Important, additional, and/or deviating data from the population described by Siqueira-Castro et al. (2009, Fig. 104r–y, Table 31): Body size in life about 90 × 40 µm; length:width ratio ranges from 2:1 to 6:1. Macronuclear nodules spherical to ellipsoidal or ovoid; sometimes dumbbell-shaped. Usually two spherical micronuclei

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← **Fig. 104k–o** *Deviata estevesi* (from Paiva & Silva-Neto 2005. Protargol impregnation). **k, l:** Infraciliature of ventral side and nuclear apparatus (of same specimen?), 94 µm. Note that the cirri of each row have been connected by a fine, dotted line by Paiva & Silva-Neto (2005); for my interpretation of the frontal ciliature, see (m, n). Arrow in (l) marks short kinety in posterior body portion which is the rear part of kinety 2 according to ontogenetic data (Fig. 104y; note similarity with *D. rositae*; Fig. 103c). **m, n:** Same figure as (k), but without fine dotted lines, to show my interpretation of the cirral pattern. Supposed frontal cirri connected by dotted line in (n); cirri originating from same anlage connected by broken line (only shown for anlagen I–III). The ontogenetic data by Siqueira-Castro et al. (2009) are not very convincing; thus, the exact origin of the anlagen and rows I–III remains unclear. **o:** Infraciliature of ventral side of early divider, 86 µm. AZM = distal end of adoral zone of membranelles, CV = contractile vacuole, LMRI, LMRO = inner (= left marginal row 1) and outer left marginal row, L1 = designation of inner left marginal row in original description, MA = macronuclear nodule, MI = micronucleus, OP = oral primordium, P = paroral, RMRI, RMRO = inner and outer right marginal row, R1, R2, R6, R7 = labelling of cirral rows in original description, I–VI = cirral rows originating from anlagen I –VI, 1, 2 = dorsal kineties. Page 609.

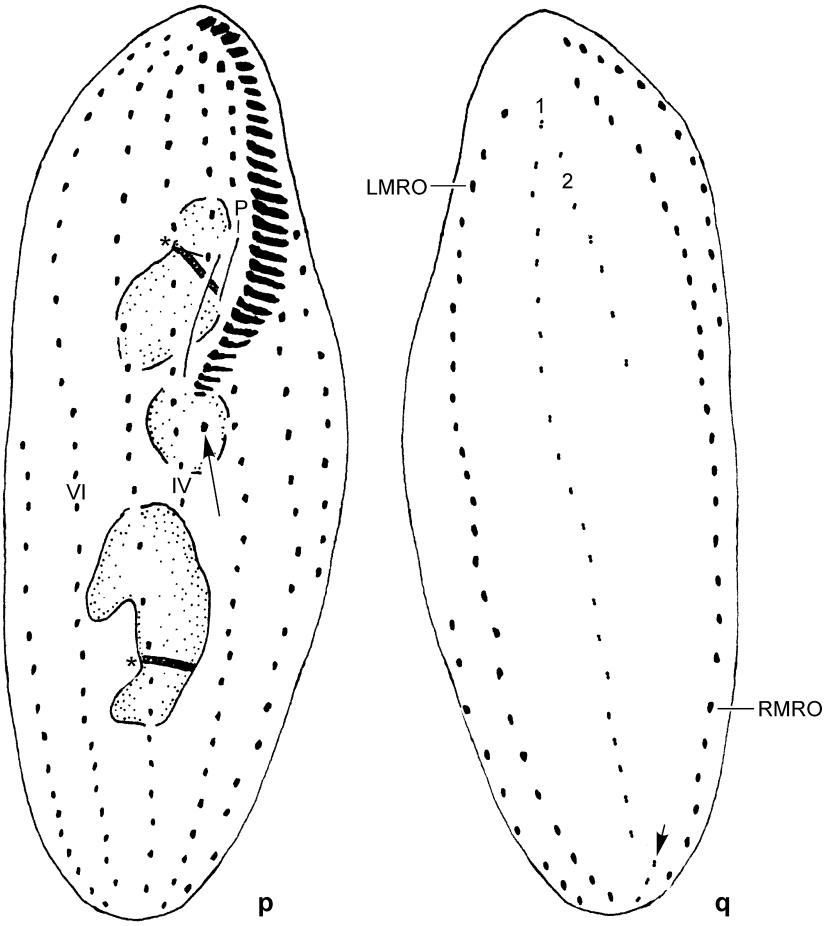


Fig. 104p, q *Deviata estevesi* (from Paiva & Silva-Neto 2005. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of a specimen with a postoral (= postperistomial) ventral cirrus (long arrow), 71 µm. Asterisks mark replication bands. Arrow in (q) denotes rear portion of kinety 2. LMRO = outer left marginal row, P = paroral, RMRO = outer right marginal row, IV, VI = frontoventral rows (possibly) originating from anlagen IV and VI, respectively, 1, 2 = dorsal kineties. Page 609.

close to each macronuclear nodule. Excretion pore of contractile vacuole on dorsal side. Cells dark a low magnification due to conspicuous compact crystals scattered through cytoplasm, alongside with variable-sized granulation; however, cortical granules lacking.

Cell division (Fig. 104o, t–y): Some stages of cell division are described by Paiva & Silva-Neto (2005) and Siqueira-Castro et al. (2009); however, important details remain fairly vague so that a detailed reinvestigation is strongly recommended. In the following description I retain the original designation of the frontoventral rows because the situation, especially in middle dividers, is rather confusing.

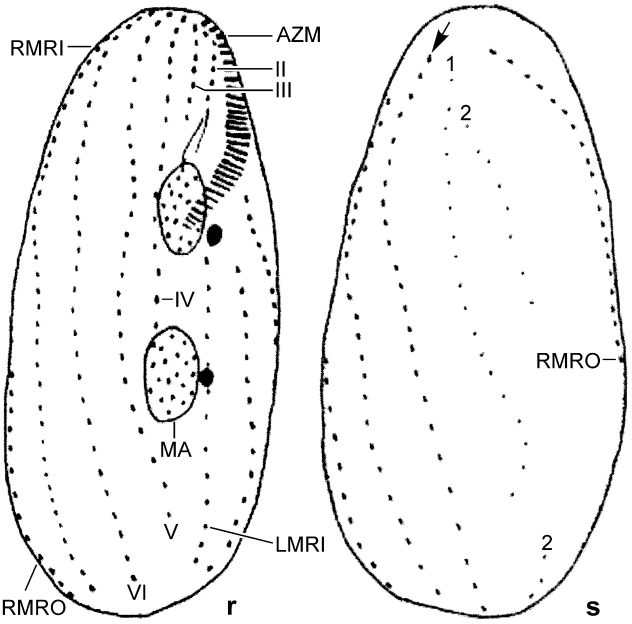


Fig. 104r, s *Deviata estevesi* (from Siqueira-Castro et al. 2009. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of same(?) specimen, 85 µm. Arrow in (s) marks outermost left marginal row (L5 in original paper). AZM = adoral zone of membranelles, LMRI = inner left marginal row (= left marginal row 1; = L1 in original paper), MA = macronuclear nodule, RMRI, RMRO = inner and outer right marginal row (R6, R7 in original paper), II–VI = frontal (II, III; R1, R2) and frontoventral (IV–VI; R3–R5) rows, 1, 2 = dorsal kineties. Page 609.

Stomatogenesis commences with the formation of an oral primordium immediately left of the rear portion of the cirral row formed by anlage IV (Fig. 104o; Paiva & Silva-Neto 2005). Siqueira-Castro et al. (2009) also reported such a parakinetal oral primordium formation; however, they also found that disaggregating cirri of row IV are involved in oral primordium formation (Fig. 104t). The undulating membrane anlage (= anlage I) originates from the right portion of the oral primordium and its distal end forms, according to Siqueira-Castro et al. (2009), row R1 (Fig. 104k). In the proter, row 1 is formed in the same way, that is, from the undulating membrane anlage. This is rather unusual and not clearly recognisable from the illustrations. In addition, this does not in agree with the situation in *Parastrongylidium oswaldi* where, as is usual, anlage I forms – besides the undulating membranes – only the left frontal cirrus (Fig. 19, 20 in Aescht & Foissner 1992).

Anlage II of the opisthe originates from anlage I, while in the proter anlage II forms within row R2 (Fig. 104w). Within rows R3 to R6 each two separated anlagen (III–IV) are formed, the anterior for the proter, the posterior for the opisthe (Fig. 104w). Within the third left marginal row from inside the anlage for the opisthe is formed (Fig. 104w). Further middle and late dividers have not been found by Siqueira-Castro et al. (2009). From a very late divider they conclude that all ventral rows replicate by within-row proliferation, forming independent anlagen in both proter and opisthe (Fig. 104x, y). The parental adoral zone of *Deviata estevesi* is not modified in the stages observed, while the old undulating membranes disaggregate to form the anlage I in early to middle dividers. In late dividers, anlage I splits longi-

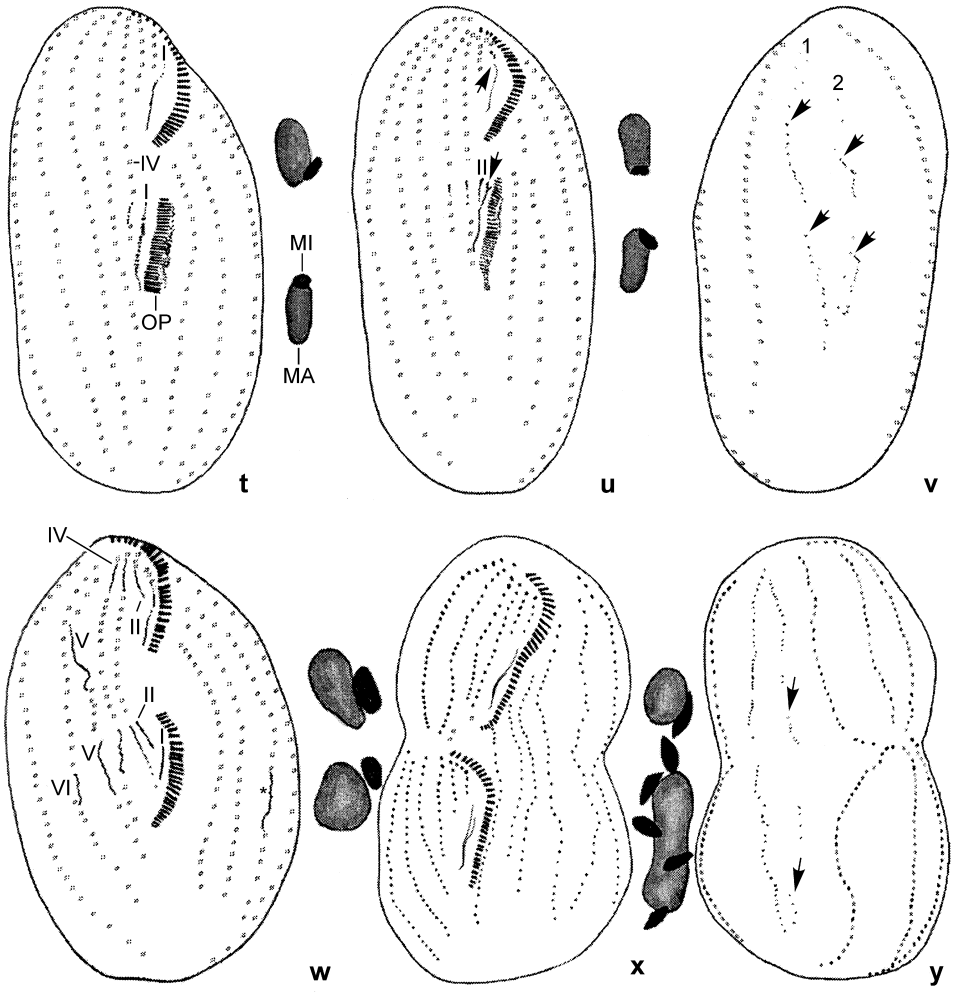


Fig. 104t–y *Deviata estevesi* (from Siqueira-Castro et al. 2009. Protargol impregnation). **t–v:** Infraciliature of ventral (t, u) and dorsal (v) side and nuclear apparatus of early dividers (u and v show same specimen), t–v = about 78 µm. Arrows in (u) mark the early primordium of frontal row "R1" (see Fig. 104k). Further details see text (note that I am not convinced that the analysis is correct in this respect; see Fig. 104n). Arrows in (v) mark dorsal kinety anlagen. **w:** Infraciliature of ventral side and nuclear apparatus of middle divider, 71 µm. Asterisk marks anlage of a left marginal row (anlage for opisthe in third row from inside). **x, y:** Infraciliature of ventral and dorsal side and nuclear apparatus of late divider, 75 µm. Note splitting of undulating membranes anlagen. Arrows in (y) mark new rear portion of dorsal kinety 2 (see also Fig. 104l, s). MA = macronuclear nodule, MI = micronucleus, OP = oral primordium, I–VI = frontal-ventral cirri anlagen, 1, 2 = dorsal kineties. Page 609.

tudinally into endoral and paroral (Fig. 104x). The parental ciliature (except the adoral zone) is likely completely resorbed during and after cell division (Siqueira-Castro et al. 2009).

Two anlagen are formed within both dorsal kineties (Fig. 104v). According to Siqueira-Castro et al. (2009), those in kinety 1 are only slightly separated, while those in kinety 2 are distinctly apart. In late dividers the anlagen in kinety 2 split and the posterior portion (3–5 basal body pairs) of each anlage migrates posteriad (Fig. 104y, arrows). This splitting is somewhat reminiscent of the dorsal kinety fragmentation in the oxytrichids where the posterior portion of the anlage formed in kinety 3 is separated from the anterior portion to form the new dorsal kinety 4. However, in the oxytrichids kinety 3 and kinety 4 are usually arranged side by side, at least partially (e.g., Fig. 6b, 24a in Berger 1999). Finally, however, the only interesting question is whether or not the processes are homologous.

Division of the nuclear apparatus proceeds in the ordinary way, that is, a replication band is formed (Fig. 104p), and the two macronuclear nodules fuse to a single mass, which later divides.

Cyst: Siqueira-Castro et al. (2009, their Fig. 3) found an "encystant" (encysting specimen), indicating that this species forms resting cysts.

Conjugation: Siqueira-Castro et al. (2009, their Fig. 6) observed conjugation, but provided no details about this part of the life cycle, except a scanning electron micrograph of a pair.

Occurrence and ecology: Limnetic. Type locality of *Deviata estevesi* is the Cabiúnas Lagoon (22°17'46.7"S 41°41'32.3"W), Macaé, Rio de Janeiro State, Brazil, where Paiva & Silva-Neto (2005) discovered it in a sample of brackish water and sediment from the bottom of the lagoon (1.2 m depth) in July 2003. The water was dark coloured due to the high concentration of detritus and humic substances. The chemical parameters were as follows: pH 7.24; dissolved oxygen 3.29 mg l^{-1}; water temperature 22.9 °C; conductivity 1875 µS; salinity 1.0 ‰. *Deviata estevesi* was not observed in the water column high above the sediment, neither was it present in samples from the same area collected in 2001 (Paiva & Silva-Neto 2005). The population described by Siqueira-Castro et al. (2009) was found in the primary settling tanks of the Penha Sewage Treatment Plant (ETE-Penha), located in the city of Rio de Janeiro, RJ, Brazil. *Deviata estevesi* occurred in 10 of 27 sewage samples and the main chemical parameters were as follows: 2.2 mg l^{-1} O_2; pH 7; 27.8 °C (likely these values are from a single measurement).

Deviata estevesi feeds on bacteria (Paiva & Silva-Neto 2005) and flagellates (Siqueira-Castro et al. 2009). It occurred together with *Coleps elongatus*, *Cristigera* sp., and some specimens of the anaerobic species *Brachonella spiralis* and *Saprodinium dentatum* (Paiva & Silva-Neto 2005). In enrichment cultures, *Deviata estevesi* was the only surviving species after 6–8 d, except for few specimens of *Cristigera* sp. and numerous individuals of *Chilodonella uncinata*, which had excysted (Paiva & Silva-Neto 2005). Siqueira-Castro et al. (2005) found it together with *Blepharisma sinuosum* and *Paramecium aurelia*.

Kahliella bacilliformis Gelei, 1954 sensu Fleury & Fryd-Versavel (1984)

1984 ***Kahliella bacilliformis*** Gelei, 1954 – Fleury & Fryd-Versavel, Protistologica, 20: 534, Fig. 4a–d, 17, 18 (Fig. 4a–d, 18 [photomicrographs of protargol-impregnated specimens] and Fig. 17 [diagram showing body length and width] are not shown in present book; site were slides deposited not mentioned).

Nomenclature: Gelei (1954) established this species in *Kahlia* Horváth, 1932 and not in *Kahliella* Corliss, 1960, as incorrectly assumed by Fleury & Fryd-Versavel (1984).

Remarks: The description of *K. bacilliformis* by Fleury & Fryd-Versavel (1984) is difficult to interpret. They made several collections from a water-filled, concreted reservoir in the forest close to the University of Orsay (France) during autumn of 1983. The reservoir contained many decomposing plants and therefore also many metopids. They cultured the specimens in wheat medium and added rice grains to support bacterial growth. In the material and method section they write that they failed to establish a clone. Thus, it is very likely that they cultured two or more species as indicated by the high variability reported for several important features, for example, body size, body outline. Likely they observed *Deviata abbrevescens* (Fig. 4a, d) as indicated by the size of the somatic cirri, which are composed of four basal bodies, and the seven cirral rows, the lower value reported by them. This identification is also supported by the late divider (Fig. 18 in Fleury & Fryd-Versavel 1984) which is more or less identical with a late divider illustrated by Eigner (1995; Fig. 96o). Fig. 4b in the French paper shows underfed specimens at the beginning of conjugation. This part of the life-cycle is, besides the mixture of two species (see below), likely also responsible for the unusual variability. The second species subsumed under *K. bacilliformis* by the French authors (Fig. 4c in Fleury & Fryd-Versavel 1984) is likely a true *Kahliella*, probably *K. simplex* with which they worked earlier (Fleury & Fryd-Versavel 1982; see p. 367 of present book). This could explain the high number of "at least three dorsal kineties" in *Deviata bacilliformis*; true *D. bacilliformis* populations have only one dorsal kinety (Table 31).

The misidentification of *Kahliella bacilliformis* by Fleury & Fryd-Versavel (1984) was already recognised by Berger & Foissner (1987, p. 201), Eigner (1995, p. 358), and Dragesco (2003). Eigner (1995) even supposed that the French population – which is obviously a mixture of two species as discussed above – represents a new *Deviata* species.

Orthoamphisiella Eigner & Foissner, 1991

1991 ***Orthoamphisiella* nov. gen.**[1] – Eigner & Foissner, Acta Protozool., 30: 129 (original description). Type species (by original designation): *Orthoamphisiella stramenticola* Eigner & Foissner, 1991.

[1] Eigner & Foissner (1991) provided the following diagnosis: Amphisiellidae with 1 row of buccal cirri and 2–3 short rows of fronto-ventral cirri left of the long ventral row.

1994 ***Orthoamphisiella* Eigner and Foissner, 1991** [1] – Shin, Dissertation, p. 47 (systematics of Korean hypotrichs).
1999 ***Orthoamphisiella* Eigner & Foissner, 1991** – Shi, Acta Zootax. sinica, 24: 254 (generic revision of hypotrichous ciliates).
1999 ***Orthoamphisiella* Eigner & Foissner, 1991** – Shi, Song & Shi, Progress in Protozoology, p. 102 (generic revision of hypotrichous ciliates).
2001 ***Orthoamphisiella* Eigner & Foissner 1991** – Aescht, Denisia, 1: 111 (catalogue of generic names of ciliates).
2001 ***Orthoamphisiella* Eigner and Foissner, 1991** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 50 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2002 ***Orthoamphisiella* Eigner and Foissner, 1991** [2] – Lynn & Small, Ciliophora, p. 453 (guide to ciliate genera).
2007 ***Orthoamphisiella* Eigner et Foissner, 1994** – Jankowski, Ciliophora, p. 452 (incorrect year; revision of ciliates).
2008 ***Orthoamphisiella* Eigner & Foissner, 1991** – Lynn, Ciliated protozoa, p. 357 (revision of ciliates).

Nomenclature: *Orthoamphisiella* is, according to Eigner & Foissner (1991), a composite of *Orthos* (Greek; straight, because of the straight cirral rows in the frontal field) and the genus-group name *Amphisiella* (for derivation, see Berger 2008, p. 85). Feminine gender (Eigner & Foissner 1991) because of the Latin suffix *-ella* (ICZN 1999, Article 30.1.3). Name-bearing type genus of the Orthoamphisiellidae Eigner, 1997. Incorrect subsequent spellings: *Orthamphisiella* and *Orthamphisiella breviseries* (NCBI GenBank; date 05 Nov 2008; Shao et al. 2007, p. 262); *Orthoamphisella breviseries* (Gong et al. 2007, p. 475); *Orthamphisiella breviseris* (Sonntag et al. 2008, p. 284).

Characterisation (A = supposed apomorphy): Non-dorsomarginalian hypotrich. Adoral zone of membranelles roughly formed like a question mark, however, distal portion does not extend onto right body margin. Undulating membranes slightly curved and arranged in parallel. Three frontal cirri, more than one buccal cirrus, a short parabuccal row, one or two short frontoventral rows, and one long frontoventral row.[3] Postoral ventral cirri, pretransverse ventral cirri, and transverse cirri lacking. One left and one right marginal row. Two more or less bipolar dorsal kineties. Dorsomarginal kineties, dorsal kinety fragmentation, and caudal cirri lacking (A?). All frontoventral cirri anlagen, except anlage I, are formed via primary primordia originating from parental ciliature (A). Terrestrial.

Additional characteristics: Body length 60–150 µm. Body outline roughly elongate elliptical. Body flexible, but not distinctly contractile in life; dorsoventrally flattened about 2:1. Contractile vacuole near left body margin about in mid-body,

[1] Shin (1994) provided the following characterisation: Elongate and long oval body with 2 rows of marginal cirri and single row of buccal cirri. Two or 3 short rows of frontoventral cirri distinct and located immediate left of long row of ventral cirri. Adoral zone of membranelles short, restricted to anterior body quarter. Usually two macronuclei present but sometimes numerous.

[2] Lynn & Small (2002) provided the following characterisation: Several cirral files to anterior left of midventral cirral file; midventral cirral file closely adjacent to right marginal cirral file; transverse cirri, absent; caudal cirri, absent.

[3] One species (*O. breviseries*) lacks the long frontoventral row. In addition, it cannot be excluded that congeners(?) with a single buccal cirrus exist (see *O. breviseries*).

Table 32 Morphometric data on *Orthoamphisiella breviseries* (bre, from Foissner et al. 2002a), *Orthoamphisiella grelli* (gre, from Eigner & Foissner 1993), and *Orthoamphisiella stramenticola* (st1, type population from Eigner & Foissner 1991; st2, Japanese population from Eigner & Foissner 1993; st3, from Shin 1994)

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	bre	47.6	48.0	6.1	1.2	12.8	38.0	60.0	25
	gre	67.8	68.0	8.9	1.8	13.1	51.0	87.0	25
	st1	93.8	92.5	6.5	1.2	6.9	78.7	105.0	29
	st2	80.7	79.0	12.4	2.5	15.4	57.0	102.0	25
	st3	114.3	115.0	7.4	2.3	6.5	103.0	126.0	10
Body, width	bre	14.8	15.0	2.0	0.4	13.5	10.0	18.0	25
	gre	23.0	21.0	3.8	0.8	16.5	16.0	31.0	25
	st1	28.8	27.5	6.6	1.2	22.9	18.7	50.0	29
	st2	28.2	27.0	5.5	1.1	19.5	21.0	43.0	25
	st3	49.5	50.0	5.6	1.8	11.4	38.0	56.0	10
Body length:width, ratio	bre	3.3	3.2	0.5	0.1	14.5	2.5	4.0	25
	st3	2.3	2.3	0.2	0.1	9.4	2.1	2.7	10
Adoral zone of membranelles, length	bre	13.6	13.0	1.7	0.3	12.6	11.0	17.0	25
	gre	22.8	22.0	1.8	0.4	7.9	19.0	27.0	25
	st1	27.5	27.5	4.6	0.8	16.7	22.5	37.5	29
	st2	29.0	29.0	3.2	0.6	11.0	24.0	37.0	25
	st3	36.6	36.5	4.1	1.3	11.3	31.0	43.0	10
Body length:length of adoral zone, ratio	bre	3.5	3.6	0.5	0.1	12.9	2.6	4.6	25
	st3	3.2	3.1	0.3	0.1	10.5	2.5	3.7	10
Undulating membranes, length [g]	st3	29.7	29.0	3.9	1.2	13.0	25.0	37.0	10
Undulating membranes length:length of adoral zone, ratio	st3	0.8	0.8	0.1	0.0	6.4	00.7	0.9	10
Anterior body end to first buccal cirrus, distance	bre	4.1	4.0	1.2	0.2	29.9	2.0	6.0	25
Anterior body end to end of parabuccal row, distance	bre	6.3	6.0	1.5	0.3	23.1	4.0	10.0	25
Rightmost (long) frontoventral row, length	bre [b]	9.3	9.0	1.7	0.3	18.5	7.0	13.0	25
	gre [b]	41.0	42.0	12.0	2.4	29.2	27.0	74.0	25
	st1 [b]	46.2	48.7	8.9	1.7	19.2	41.2	83.7	27
	st2 [b]	46.7	46.0	7.9	1.6	17.0	31.0	66.0	25
Anterior body end to first macronuclear nodule, distance	bre	9.3	9.0	2.4	0.5	25.5	5.0	15.0	25
First macronuclear nodule from front, length	bre [f]	30.2	31.0	4.7	0.9	15.6	22.0	38.0	25
	gre	13.0	12.0	3.2	0.6	24.6	9.0	20.0	25
	st1	10.9	11.3	1.7	0.4	15.2	6.8	13.8	22
	st2	10.0	10.0	2.4	0.5	24.0	6.0	15.0	25
	st3 [h]	12.4	12.0	1.7	0.5	13.8	9.0	15.0	10
First macronuclear nodule from front, width	gre	6.0	6.0	1.2	0.2	20.0	4.0	9.0	25
	st1	5.9	6.3	0.9	0.2	15.2	3.8	7.5	22
	st2	5.7	6.0	0.6	0.1	10.5	5.0	7.0	25
	st3 [h]	8.1	8.0	1.1	0.3	13.3	7.0	10.0	10
Second macronuclear nodule from front, length	gre	11.9	12.0	2.9	0.6	24.4	6.0	17.0	24
	st1	11.9	12.5	3.0	0.6	25.2	5.0	17.5	28
	st2	7.5	6.5	2.2	0.4	29.3	5.0	15.0	25
Second macronuclear nodule from front, width	gre	5.9	6.0	1.0	0.2	16.9	4.0	9.0	24
	st1	5.3	5.0	0.9	0.2	16.9	3.7	7.5	29
	st2	5.2	5.0	0.6	0.1	11.5	4.0	6.0	25

Table 32 Continued

Characteristics[a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Adoral membranelles, number	bre	20.6	20.0	1.4	0.3	7.0	19.0	25.0	21
	gre	20.3	21.0	1.2	0.2	5.9	18.0	22.0	25
	st1	20.4	20.0	2.7	0.6	13.2	18.0	30.0	23
	st2	23.2	24.0	1.9	0.4	8.2	19.0	26.0	25
	st3	24.0	23.0	1.9	0.6	8.1	23.0	28.0	10
Macronuclear nodules, number	bre			see text					
	gre	2.1	2.0	–	–	–	1.0	3.0	25
	st1	4.3	4.0	0.6	0.1	13.9	4.0	6.0	30
	st2	4.0	4.0	0.0	0.0	0.0	4.0	4.0	25
	st3	4.0	4.0	0.0	0.0	0.0	4.0	4.0	10
Anterior micronucleus, length	bre	1.8	1.6	–	–	–	1.4	2.5	20
	st3[i]	2.2	2.0	0.3	0.1	15.7	1.5	2.5	10
Anterior micronucleus, width	bre	1.7	1.6	–	–	–	1.4	2.0	20
Micronuclei, number	bre	1.6	2.0	–	–	–	1.0	3.0	19
	gre	2.5	2.0	1.2	0.3	48.0	1.0	6.0	23
	st1	5.1	5.0	1.3	0.2	25.4	3.0	7.0	28
	st2	4.8	5.0	1.5	0.3	31.2	3.0	8.0	25
	st3	3.8	4.0	0.6	0.2	16.6	3.0	5.0	10
Frontal cirri, number	bre	3.0	3.0	0.0	0.0	0.0	3.0	3.0	24
	st3	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
Frontoventral rows, number	bre[k]	2.1	2.0	–	–	–	2.0	3.0	25
Buccal cirri, number	bre	2.5	2.0	–	–	–	2.0	4.0	25
	gre	2.1	2.0	–	–	–	2.0	3.0	25
	st1	4.7	5.0	1.0	0.2	21.2	4.0	7.0	22
	st2	3.5	3.0	–	–	–	3.0	4.0	25
	st3	3.1	3.0	0.3	0.1	10.2	3.0	4.0	10
Parabuccal cirri, number	bre[c]	2.7	3.0	0.7	0.1	27.1	1.0	4.0	25
	gre[c]	2.2	2.0	0.5	0.1	22.7	1.0	3.0	25
	st1[c]	3.7	4.0	0.7	0.1	18.9	3.0	5.0	22
	st2[c]	3.0	3.0	0.5	0.1	16.6	2.0	4.0	25
	st3[j]	7.5	7.5	1.1	0.3	14.4	6.0	9.0	10
Short frontoventral row next to parabuccal row, number of cirri	gre[d]	3.0	3.0	0.5	0.1	16.7	2.0	4.0	25
	st1[d]	4.0	4.0	0.6	0.1	15.0	3.0	5.0	23
	st2[d]	3.6	4.0	0.6	0.1	16.7	3.0	5.0	25
Additional short frontoventral row, number of cirri	bre[e]	3.7	4.0	1.5	0.9	41.7	2.0	5.0	3
	gre[e]	2.6	3.0	0.8	0.3	30.8	1.0	4.0	10
	st1[e]	2.8	3.0	1.0	0.2	35.7	1.0	5.0	15
	st2[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25
Rightmost (long) frontoventral row, number of cirri	bre[b]	4.8	5.0	0.7	0.1	15.4	3.0	7.0	25
	gre[b]	18.2	18.0	1.7	0.4	9.3	14.0	22.0	23
	st1[b]	22.8	23.0	2.4	0.5	10.5	19.0	30.0	20
	st2[b]	19.7	20.0	1.6	0.3	8.1	16.0	22.0	25
	st3[b]	20.7	20.5	3.4	1.1	16.3	17.0	27.0	10
Right marginal row, number of cirri	bre	31.6	31.0	2.1	0.4	6.7	26.0	37.0	25
	gre	26.4	26.0	2.4	0.5	9.1	20.0	31.0	25
	st1	40.7	41.0	2.1	0.5	5.1	36.0	44.0	19
	st2	28.2	28.0	2.0	0.4	7.1	24.0	32.0	25
	st3	31.4	31.0	3.5	1.1	11.3	24.0	37.0	10
Left marginal row, number of cirri	bre	28.5	28.0	2.6	0.5	9.2	20.0	32.0	25
	gre	22.6	23.0	2.7	0.5	11.9	18.0	28.0	25

Table 32 Continued

Characteristics [a]	Species	Mean	M	SD	SE	CV	Min	Max	n
Left marginal row, number of cirri	st1	33.5	34.0	2.3	0.5	6.9	30.0	38.0	21
	st2	24.3	24.0	2.6	0.5	10.7	18.0	30.0	25
	st3	29.3	29.5	2.4	0.8	8.2	25.0	33.0	10
Dorsal kineties, number	bre	2.0	2.0	0.0	0.0	0.0	2.0	2.0	24
	gre	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	st1	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	st2	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	st3	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
Dorsal kinety 1, number of basal body pairs	bre	7.9	8.0	1.3	0.3	16.0	6.0	11.0	19
Dorsal kinety 2, number of basal body pairs	bre	7.6	8.0	1.0	0.2	13.6	5.0	9.0	18

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known; if two values are known then they are listed as Min and Max; if only one value is known then it is listed as Mean), SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] Termed "Ventral row" and/or "Long ventral (median) row" in original description of *O. stramenticola* (Eigner & Foissner 1991) and *O. grelli* (Eigner & Foissner 1993). Termed "Row of midventral cirri" (RFVC in Table 5 of Shin 1994) in description of Korean population of *O. stramenticola*. Termed "Frontoventral row 2" in *O. breviseries* (note that this row is not elongated in this species, Fig. 107h, j).

[c] Termed "Fronto-ventral row 1" in original descriptions (Eigner & Foissner 1991, 1993; Foissner et al. 2002a).

[d] Termed "Fronto-ventral row 2" in original descriptions (Eigner & Foissner 1991, 1993; Foissner et al. 2002a).

[e] Termed "Fronto-ventral row 3" in original descriptions (Eigner & Foissner 1991, 1993; Foissner et al. 2002a). Note that this row is lacking in Japanese population of *O. stramenticola* and occurs very rare in *O. breviseries*.

[f] In *O. breviseries* the length of the nuclear figure is given.

[g] Likely the distance between the anterior end of the paroral and the posterior end of the endoral is given.

[h] It is not indicated which nodule (anteriormost, posteriormost, ...) was measured.

[i] Diameter is given; it is not indicated which micronucleus (anteriormost, posteriormost, ...) was measured.

[j] Comprises the cirri of the parabuccal row and the short frontoventral row right of it.

[k] Buccal row not included.

during diastole with indistinct canals. Cortical granules lacking. Movement without peculiarities. Undulating membranes more or less straight, roughly arranged in parallel, that is, not intersecting optically; paroral commences more anteriorly than endoral. Cirri about 10 µm long. Three slightly enlarged frontal cirri form transverse pseudorow. Dorsal bristles about 3 µm long.

Remarks: Eigner & Foissner (1991) assigned *Orthoamphisiella* to the Amphisiellidae – obviously because of the long frontoventral row – and compared it with taxa like *Amphisiella*, *Amphisiellides*, *Paramphisiella*, and *Hemiamphisiella* (comparisons see below). The cell division of the type species was analysed by Eigner & Foissner (1993). The long frontoventral row is formed from a single anlage, whereas in the amphisiellids it originates from the two or three rightmost anlagen (for review of amphisiellids, see Berger 2008). Thus, they stated that *Orthoamphisiella* is misplaced in the amphisiellids, but did not propose a new classification (Eigner & Foissner 1993, p. 345). To eliminate this misclassification, Eigner (1997) established the Orthoamphisiellidae (details see below). By contrast, Shi et al. (1999), Lynn & Small (2002), Jankowski (2007), and Lynn (2008) took over the original classification of *Orthoamphisiella* in the Amphisiellidae, that is, they synonymised the Orthoamphisiellidae with the Amphisiellidae.

I am very uncertain about the higher level classification of *Orthoamphisiella*. An assignment to the amphisiellids makes no sense because of the different formation of the frontoventral row (from single anlage vs. from two or three). In addition, in *Orthoamphisiella* the frontoventral row of the proter is a composite of parental cirri (anterior portion) and newly formed cirri (posterior portion; Fig. 105r), which is a further distinct difference to the amphisiellids, where all portions are newly formed. Because of the preservation of parental cirri one could assign *Orthoamphisiella* to the "melting pot" Kahliellidae. An alternative is the classification as incertae sedis in the paraphyletic assemblage "non-dorsomarginalian hypotrichs" because a dorsomarginal kinety is lacking. However, it has to be emphasised that both classifications are rather vague and not well founded. For a foundation of the non-use of the Orthoamphisiellidae, see next chapter. Unfortunately, we do not have support from molecular data because so far gene sequence analyses have only been made for *O. breviseries*, a species whose assignment to *Orthoamphisiella* is uncertain according to the morphology. Thus, gene sequence data of the type species are needed to get a better idea which of the proposed classifications (Amphisiellidae, Orthoamphisiellidae, Kahliellidae, others) is the most suitable one.

As briefly mentioned above, Eigner & Foissner (1993) compared *Orthoamphisiella* with several amphisiellid genera. *Amphisiella* Gourret & Roeser, 1888 is the type genus of the Amphisiellidae. It is confined to marine habitats and produces the long frontoventral row (= amphisiellid median cirral row) from the two (or three) rightmost anlagen (for review, see Berger 2008, p. 84).

Amphisiellides atypicus (Hemberger, 1985) Foissner, 1988, the sole species of this genus, has very likely a dorsal kinety fragmentation and was therefore classified in the oxytrichids by Berger (2008, p. 651). The long frontoventral row is formed from a single anlage, which is indeed reminiscent of *Orthoamphisiella*. More detailed ontogenetic data and molecular studies are needed to find the true phylogenetic position of this genus. A synonymy of *Amphisiellides* and *Orthoamphisiella* can be excluded because *A. atypicus* has distinct transverse cirri (vs. lacking).

In *Paramphisiella* Foissner, 1988 the long frontoventral row originates from the two rightmost cirral anlagen, a feature assigning it to the amphisiellids (for review, see Berger 2008, p. 351).

Afroamphisiella Foissner et al., 2002a also has a very similar ventral and dorsal infraciliature (for review, see Berger 2008, p. 371). Unfortunately, the formation of the long, rightmost frontoventral row is not known in *A. multinucleata* Foissner et al., 2002a and *A. abdita* (Foissner, 1997) Foissner et al., 2002a. However, this long row participates in the formation of the oral primordium, whereas this primordium originates de novo in *Orthoamphisiella*, indicating that these two genera are not very closely related (Fig. 105j–m).

The three species assigned to *Orthoamphisiella* were found in terrestrial habitats in Austria, Japan, Korea, Saudi Arabia, Namibia, and Gough Island, indicating that it is a group of not very common, but cosmopolitan soil inhabitants.

Foundation for the non-use of the Orthoamphisiellidae: Eigner (1997, p. 557) established the family Orthoamphisiellidae[1] comprising 10 species. The type species of this group is *Orthoamphisiella stramenticola* which, indeed, shows curious features: (i) All frontoventral cirri anlagen (except anlage I) of both proter and opisthe are formed from primary primordia, which originate within the parental frontoventral rows. Only anlage I of the opisthe is formed from the oral primordium (Fig. 105l–p). (ii) The anterior portion of the primary primordium in the long frontoventral row becomes the rear portion of the long frontoventral row of the proter while the posterior portion forms the whole long frontoventral row of the opisthe. The anterior portion of the parental long frontoventral row is retained or renewed (likely this means reorganised) and forms the anterior portion of the frontoventral row of the proter (Fig. 105r). If this observation is correct, then the anteriormost cirri of the proter must be, at least in some cases, very old (reinvestigation of ontogenesis thus recommended). These two features are in fact highly characteristic and are very likely apomorphies; the question is at which level? In the following paragraphs the eight species belonging to the orthoamphisiellids according to Eigner (1997) are briefly discussed.

Parastrongylidium oswaldi Aescht & Foissner, 1992. Remarks: Aescht & Foissner (1992) illustrated some morphogenetic stages clearly showing that within all parental rows two anlagen, which are clearly separated by parental cirri, are formed; that is, primary primordia, the main feature of the name-bearing type genus, are not present in *P. oswaldi* (Fig. 19, 20 in Aescht & Foissner 1992).

Cladotricha koltzowii Gaievskaïa, 1925 and *Cladotricha halophila* Wilbert, 1995. Remarks: In both species two anlagen are formed within each frontoventral row

[1] Eigner (1997) provided the following diagnosis: The two rightmost ventral cirral rows develop each by one within anlage. Dorsomarginal kineties, split dorsal kineties and transverse cirri absent. Remarks: Unfortunately, the diagnosis is equivocal. One interpretation (mainly derived from the name-bearing type genus) is that within the two rightmost frontoventral rows each one primary primordium (= one anlage which separates to form the secondary primordia) is formed (Fig. 105m–p). A second interpretation is that within the two rightmost frontoventral rows ordinary within anlagen (two per row) occur.

(Fig. 43r, 49i, k). In addition, the anlagen II and III of the opisthe are formed, as is usual, from the oral primordium.

Orthoamphisiella franzi (Foissner, 1982) Eigner, 1995. Remarks: Within the parental frontoventral row V two anlagen are formed in this species, which is now the type of the new genus *Neowallackia* (Fig. 53l, n). In addition, at least two anlagen are formed from the oral primordium (Fig. 53f, h).

Trachelochaeta gonostomoida Hemberger, 1985. Remarks: In this species the formation of the long frontoventral row proceeds indeed very similar as in *Orthoamphisiella stramenticola*, except that no parental cirri are retained (Fig. 124d–f in Berger 1999). However, the oral apparatus is identical as in *G. affine*, type of *Gonostomum*. Thus, I removed it from *Trachelochaeta* (p. 300) and transferred it to *Gonostomum* (Berger 1999, p. 392; p. 58 in present book), which is the name-bearing type of the Gonostomatidae.

Engelmanniella mobilis (Engelmann, 1862) Foissner, 1982. Remarks: This species has, like *Orthoamphisiella stramenticola*, a long frontoventral row (Fig. 87c). However, the anlagen for the proter and the opisthe originate independently within this row. In addition, the anlagen I–III of the opisthe are formed from the oral primordium (Fig. 89e, h). These significant differences to *Orthoamphisiella* are supported by molecular data, which assign *E. mobilis* and *O. breviseries*, which is, however, not the type species, to rather different clades (e.g., Sonntag et al. 2008). Eigner (1999, p. 46) obviously has removed *Engelmanniella* from the orthoamphisiellids.

Psilotricha succisa (Müller, 1786) Foissner, 1983. Remarks: Now *Urospinula succisa* (Müller, 1786) Esteban et al., 2001. This species is a non-dorsomarginalian hypotrich which forms the frontoventral rows very likely not via primary primordia, and the anlagen I and II of the opisthe originate from the oral primordium (Foissner 1983). These are distinct differences to *Orthoamphisiella* indicating that *U. succisa* is not very closely related to *Orthoamphisiella*. Eigner (1999, p. 46) obviously has removed *U. succisa* from the orthoamphisiellids.

Circinella arenicola Foissner, 1994. Remarks: In this species the anlagen for the frontoventral row are not formed within the parental row and the leftmost anlagen of the opisthe originate from the oral primordium (Fig. 59e–j) so that a classification in the orthoamphisiellids is inexplicable. Later, Eigner (1999, p. 46) did not consider *Circinella* in the phylogenetic analyses of the orthoamphisiellids.

The previous paragraphs show that actually non of the taxa originally included in the orthoamphisiellids has the curious features (all anlagen, except I, are formed from primary primordia originating in parental rows; anterior portion of long frontoventral row of proter composed of parental cirri) of the name-bearing type *O. stramenticola*. Thus, the Orthoamphisiellidae would be monotypic, that is, redundant. The formation of within-anlagen in the two rightmost anlagen is likely not sufficient enough to define the group. Consequently, I do not use this suprageneric taxon in the present review. However, when the (true) sistergroup and further related taxa of *Orthoamphisiella* are known, then a reactivation of the group is justified.

Species included in *Orthoamphisiella* (alphabetically arranged basionyms are given): (1) *Orthoamphisiella grelli* Eigner & Foissner, 1993; (2) *Orthoamphisiella stramenticola* Eigner & Foissner, 1991 (type species). Incertae sedis: (3) *Orthoamphisiella breviseries* Foissner, Agatha & Berger, 2002. *Orthoamphisiella breviseries* lacks the long, rightmost frontoventral row. Thus, it is classified as incertae sedis in the present genus (details see remarks of this species).

Species misplaced in *Orthoamphisiella*: The following species was assigned to *Orthoamphisiella*.

Orthoamphisiella franzi (Foissner, 1982) Eigner, 1995. Remarks: Now it is the type species of *Neowallackia* (p. 281).

Key to *Orthoamphisiella* species

When you know that your specimen/population belongs to *Orthoamphisiella*, species identification is rather simple and mainly based on the nuclear apparatus. If you are not successful with the key below, see also *Afroamphisiella*, *Lamtostyla*, and *Hemiamphisiella* (for review of these genera, see Berger 2008).

1 Usually 4 macronuclear nodules (Fig. 105a, j, u, w). . . . . *Orthoamphisiella stramenticola* (p. 628)
- Two (rarely 3) macronuclear nodules or only one macronucleus (Fig. 106a, 107a, e, g, i, j). **2**

2 Two macronuclear nodules; rightmost frontoventral row extends to near cell centre (Fig. 106a, c).. . . . . *Orthoamphisiella grelli* (p. 639)
- One dumb-bell-shaped macronucleus; rightmost frontoventral row does not extend beyond level of proximal end of adoral zone (Fig. 107a, e, g, h, j). . . . . *Orthoamphisiella breviseries* (p. 642)

Orthoamphisiella stramenticola Eigner & Foissner, 1991 (Fig. 105a–w, Table 32)

1991 ***Orthoamphisiella stramenticola* nov. spec.**[1] – Eigner & Foissner, Acta Protozool., 30: 131, Fig. 1, 6–13, Table 1 (Fig. 105a–h; original description; according to Eigner & Foissner 1991, a holotype [accession number 1993/31] and a paratype [1993/32] slide are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; for details, see nomenclature).

1993 ***Orthoamphisiella stramenticola*** – Eigner & Foissner, Arch. Protistenk., 143: 340, Fig. 1–12, Table 1 (Fig. 105i–t; description of Japanese population and cell division).

1994 ***Orthoamphisiella stramenticola* Eigner and Foissner, 1991** – Shin, Dissertation, p. 47, Fig. 4A–C, Table 5 (Fig. 105u–w; description of a Korean population).

[1] Eigner & Foissner (1991 provided the following diagnosis: Size in vivo 80–140 × 30–45 µm. Body shape almost rectangular. 4 macronuclear segments, 20 adoral membranelles, 5 buccal cirri and 10 frontoventral cirri in 2–3 rows on average.

1997 ***Orthoamphisiella stramenticola* Eigner & Foissner, 1991** – Eigner, J. Euk. Microbiol., 44: 557, Fig. 9 (Fig. 105e; schematic representation of cell division [the schematic figure is not shown in present book]).

1998 ***Orthoamphisiella stramenticola* Eigner and Foissner, 1991** – Shin, Korean J. syst. Zool., 14: 386, Fig. 2A–C, Table 1 (Fig. 105u–w; description of Korean population studied by Shin 1994).

1999 ***Orthoamphisiella stramenticola* Eigner & Foissner, 1991** – Shi, Progress in Protozoology, p. 254, Fig. 19A, B (slightly schematic redrawing of Fig. 105e; generic revision of hypotrichous ciliates).

1999 ***Orthoamphisiella stramenticola* Eigner & Foissner, 1991** – Shi, Song & Shi, Progress in Protozoology, p. 102, Fig. 20A, B (slightly schematic redrawing of Fig. 105e; generic revision of hypotrichous ciliates).

2001 ***Orthoamphisiella stramenticola* Eigner and Foissner, 1991** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 50 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2002 ***Orthoamphisiella stramenticola*** – Lynn & Small, Ciliophora, p. 453, Fig. 39A, B (Fig. 105e, f; guide to ciliate genera).

2007 ***Orthoamphisiella stramenticola*** – Jankowski, Ciliophora, p. 453, Fig. 285 (Fig. 105i, j; revision of ciliates; the illustrations provided are not from Eigner & Foissner 1991, but from Eigner & Foissner 1993).

Nomenclature: The species-group name *stramenticola* (living in the litter; Eigner & Foissner 1991) is a composite of the Latin substantive *stramentum* (litter, straw), the thematic vowel *-i-*, and the Latin verb *colere* (to live in). Usually, species-group names ending with *-cola* are considered as appositive substantives and are thus not changed when transferred to a genus of different gender (Werner 1972, p. 138). Type species of *Orthoamphisiella* Eigner & Foissner, 1991.

Eigner & Foissner (1991, p. 131) deposited "a holotype and a paratype of *O. stramenticola* as 2 slides of protargol impregnated cells ..." in the museum in Linz (LI). However, according to Aescht (2008, p. 180) on the "holotype" slide (accession number 1993/31) three specimens, and not only a single individual as challenged in the ICZN (1999, Article 73.1), are marked with arrows (Fig. 22 in Aescht 2008). In addition, none of the specimens illustrated is designated as holotype specimen in the original description (Fig. 105e, f, g, h; Eigner & Foissner 1991). Consequently, the three specimens on the marked slide 1993/31 are syntypes (= symphoronts according to the terminology used by Aescht 2008). However, since Eigner & Foissner (1991) used a clone (see occurrence and ecology section), the term holotype is perhaps applicable to all specimens.

Shin (1994, 1998) studied 10 live specimens and 10 protargol-impregnated individuals. I did not find a hint where the permanent slides have been deposited; likely in the Department of Molecular Biology at the Seoul National University where M. K. Shin made his dissertation.

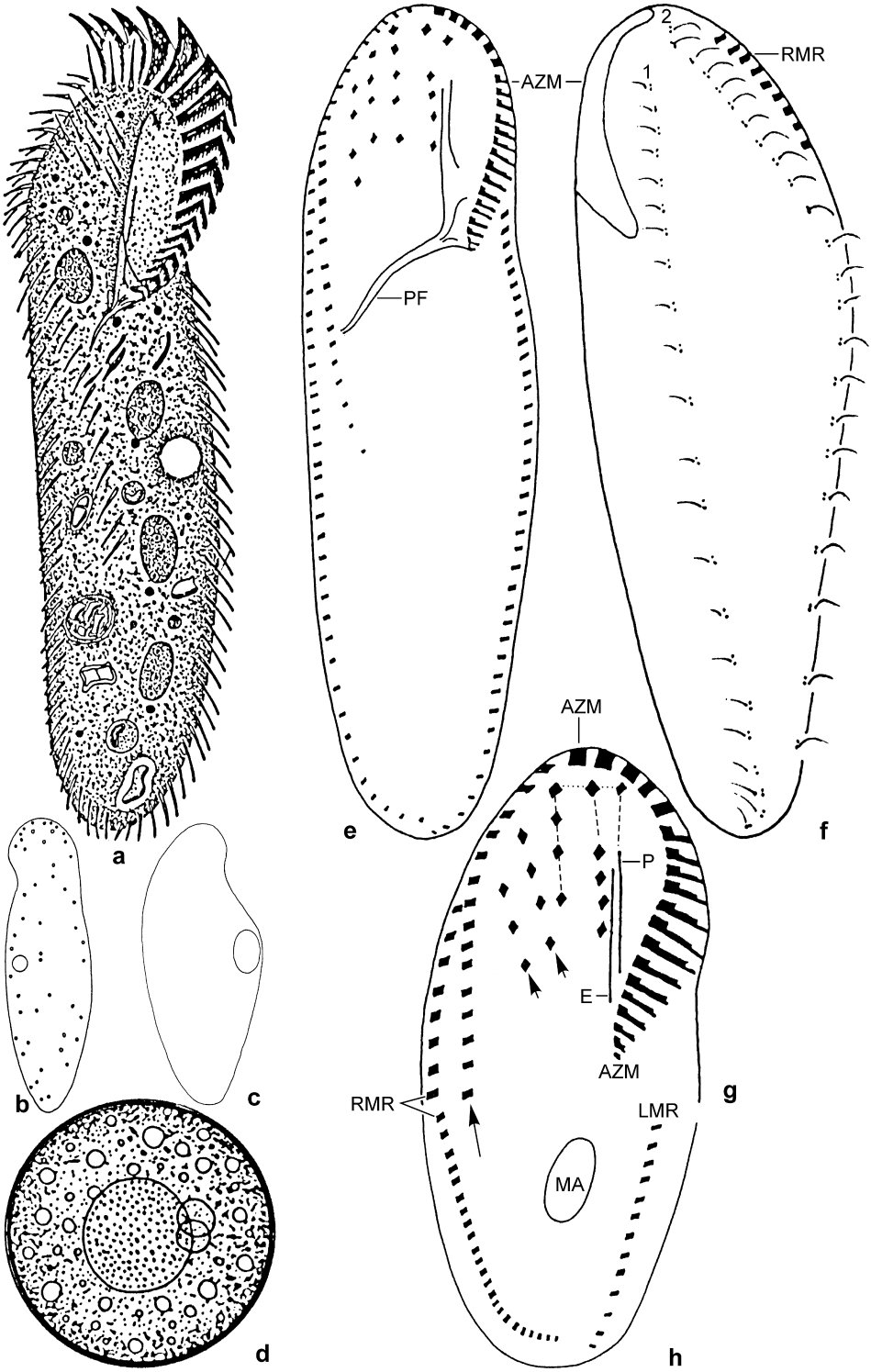
Remarks: *Orthoamphisiella stramenticola* has cortical granules according to the original description (Fig. 105b; Eigner & Foissner 1991, p. 131). Eigner & Foissner (1993, p. 340) reinvestigated the type population and found that these granules were actually mitochondria, that is, the type species lacks, like the congeners, cortical granules.

For comparison with *O. grelli*, see there. *Orthoamphisiella breviseries* lacks the long frontoventral row and has a single, dumbbell-shaped macronucleus (Fig. 107a, g, e). Eigner & Foissner (1991) recognised that *Lamtostyla quadrinucleata* (Berger & Foissner, 1989) Berger, 2008 is very similar to *O. stramenticola* as concerns the frontoventral and dorsal ciliature and the nuclear apparatus. However, it has transverse cirri so that synonymy of these two species can be excluded (Berger 2008, p. 190). Ontogenetic data of *L. quadrinucleata* are lacking; when they reveal that the rightmost frontoventral row is formed as in *Orthoamphisiella* from a single anlage and not as in the amphisiellids from two or three anlagen, then it should be removed from the amphisiellids, classified in a new genus, and the orthoamphisiellids could be reactivated. The same is true for *Lamtostyla vitiphila* (Foissner, 1987) Berger, 2008, which also has transverse cirri, only each one buccal and parabuccal cirrus, and three dorsal kineties (for review, see Berger 2008, p. 187). *Hemiamphisiella quadrinucleata* (Foissner, 1984) Foissner, 1988 has caudal cirri and four dorsal kineties, including a dorsomarginal kinety (for review, see Berger 2008, p. 318), indicating that it cannot be closely related with *Orthoamphisiella*.

Shin (1994, p. 220) made a phenetic analysis based on 20 species and 24 features. Accordingly, *Orthoamphisiella stramenticola* clusters with *Amphisiella acuta* (for review, see *Paramphisiella acuta* in Berger 2008, p. 352) and *Holostichides chardezi* (for review, see Berger 2006, p. 594). However, *Paramphisiella acuta* is (very likely) an amphisiellid and *H. chardezi* is certainly a urostyloid, indicating that the analysis does not reflect the real phylogenetic relationships.

Morphology: At first the clonal type population from Austria is described (Fig. 105a–h, Table 32; Eigner & Foissner 1991); in the last two paragraphs of the morphology section, additional and/or deviating data from the Japanese population studied by Eigner & Foissner (1993; Table 32) and the Korean population investigated by Shin (1994, 1998; Fig. 105u–w, Table 32) are provided. Eigner & Foissner (1993) studied the ontogenesis of a second population from the type locality. These specimens have somewhat more cirri in the rightmost (long) frontoventral row (mean = 28, Min = 26, Max = 32, n = 12) than the type population (mean = 23). According to Eigner & Foissner (1993), this is perhaps due to different population types (clonal type population versus specimens from raw culture).

Fig. 105a–h *Orthoamphisiella stramenticola* (from Eigner & Foissner 1991. a–d, from life; e–h, protargol impregnation). **a:** Ventral view of representative specimen, 107 µm. **b:** Shape variant. Note that the loosely arranged cortical ("subpellicular" in original description) granules described and illustrated by Eigner & Foissner (1991) are a misobservation, that is, *Orthoamphisiella stramenticola* lacks cortical granules (see text). **c:** Body outline of a middle divider in ventral view. **d:** Resting cyst, 20 µm. **e, f:** Infraciliature of ventral and dorsal side of two specimens, e = 100 µm. **g, h:** Infraciliature of anterior and posterior portion of ventral side of same(?) specimen. Frontal cirri connected by dotted line. Cirri originating from same anlage connected by broken line (only shown for anlagen I–III). Short arrows mark short frontoventral rows, long arrow denotes long, rightmost frontoventral row. AZM = adoral zone of membranelles, E = endoral, LMR = left marginal row, MA = macronuclear nodule, P = paroral, PF = pharyngeal fibres, RMR = right marginal row, 1, 2 = dorsal kineties. Page 628. →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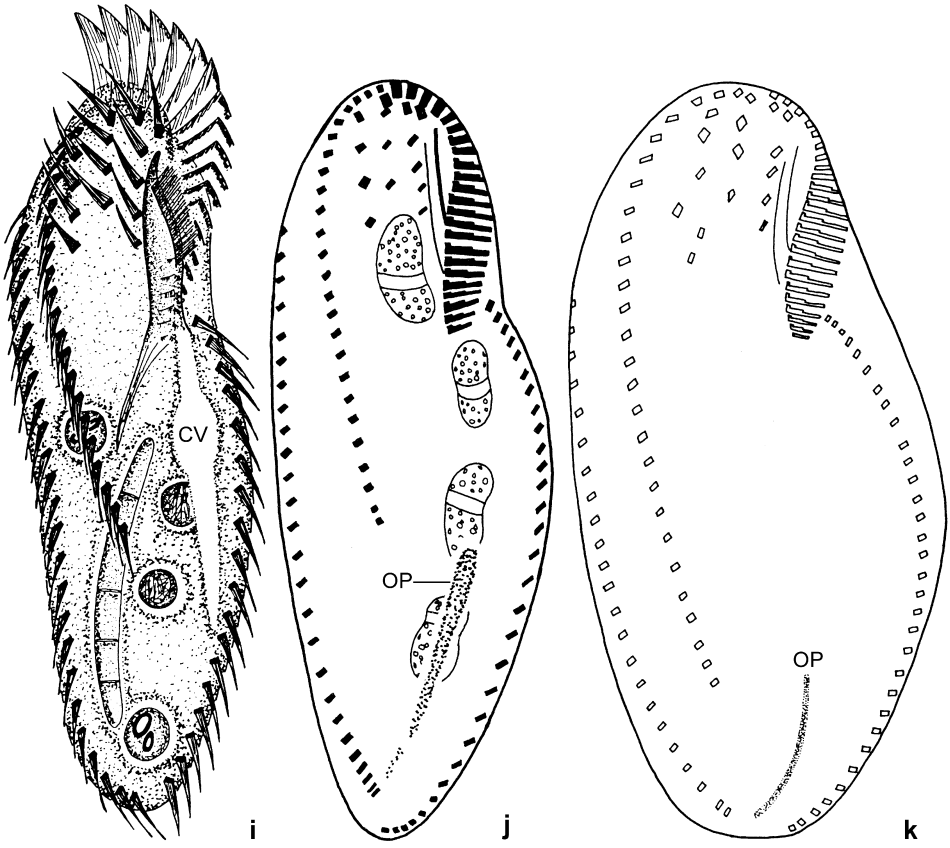


Fig. 105i–k *Orthoamphisiella stramenticola* (from Eigner & Foissner 1993. i, from life; j, k, protargol impregnation. i, j, Japanese population; k, Austrian population). **i:** Ventral view of interphasic specimen, 80 µm. **j, k:** Infraciliature of ventral side and nuclear apparatus of early dividers, j = 87 µm, k = 82 µm. Obviously, the oral primordium originates de novo, that is, without contact to parental infraciliature (details see text). CV = contractile vacuole, OP = oral primordium. Page 628.

Body size of type population 80–140 × 30–45 µm; body length:width ratio 3.3:1 on average in protargol preparations (Table 32). Body outline roughly rectangular; right margin straight to slightly convex, left somewhat indented behind adoral zone of membranelles; both ends broadly rounded, sometimes anterior portion head-like narrowed, and posterior one pointed (Fig. 105a, b). Body dorsoventrally flattened about 2:1; under coverglass pressure slightly contractile. Usually four macronuclear nodules; anteriormost nodule globular and arranged right of proximal portion of adoral zone; other nodules ellipsoidal and placed left of midline; chromatin bodies spherical. On average five globular micronuclei near macronuclear nodules (Fig. 105a). Contractile vacuole about in mid-body near left body margin; during diastole without collecting canals. Cortical granules lacking (see remarks). Cytoplasm with

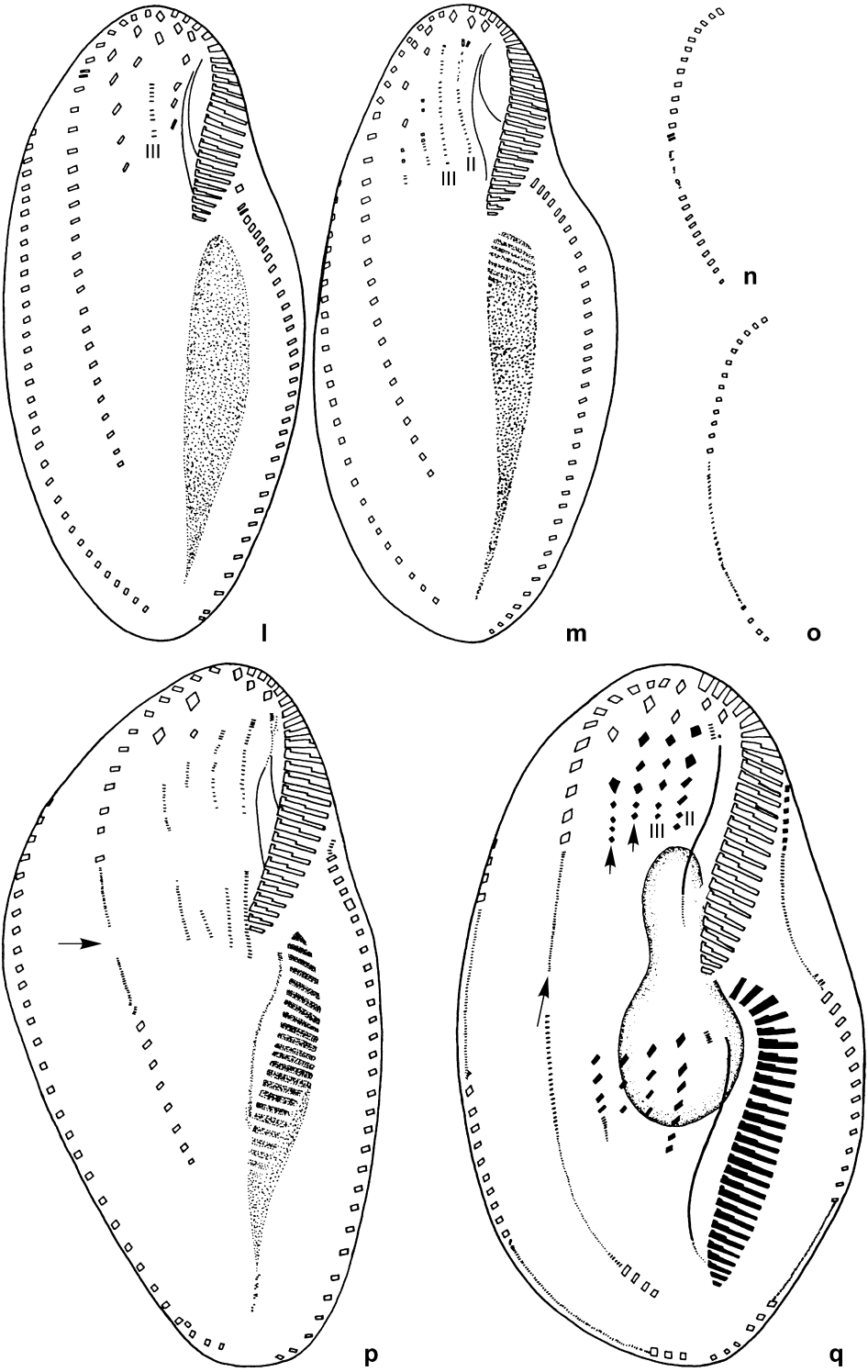
crystals and greasily shining globules. Food vacuoles 3–7 µm across. Cytopyge at posterior end of cell. Moves fast and changes direction often.

Adoral zone of membranelles occupies about 30% of body length, composed of 20 membranelles of ordinary fine structure on average (Fig. 105a, e, g, Table 32). Cilia of adoral membranelles 13–17 µm long in life. Buccal area not described, moderately large according to Fig. 105a, e. Undulating membranes more or less straight and arranged in parallel; both commence about at level of anterior end of buccal cirri row; paroral obviously shorter than endoral (Fig. 105e, g). Pharyngeal fibres extend rightwards.

Cirral pattern rather variable, mainly due to the presence of a third, short frontoventral row in 64% of specimens (Fig. 105a, e, g, Table 32). All cirri 8–12 µm long. Frontal cirri slightly enlarged, arranged in more or less transverse pseudorow with left cirrus ahead of undulating membranes. Usually five buccal cirri right of undulating membranes with front cirrus at level of second parabuccal cirrus or anterior end of paroral. On average four parabuccal cirri (termed fronto-ventral row 1 in original description) behind right frontal cirrus. Frontoventral row next to parabuccal row (fronto-ventral row 2 in original description) composed of four cirri on average, terminates about at same level as parabuccal row (Fig. 105e) or somewhat behind (Fig. 105g). As mentioned above, 64% of specimens analysed with additional, short frontoventral row (fronto-ventral row 3 in original description); composed of 1–5, on average three cirri (right short arrow in Fig. 105g). Rightmost (long) frontoventral row begins right of distal end of adoral zone, terminates at 50% of body length and composed of 23 cirri on average (Fig. 105a, e, g, Table 32). Last cirri of frontoventral rows sometimes out of line. Postoral ventral cirri, pretransverse ventral cirri, and transverse cirri lacking. Right marginal row commences dorsolaterally about at level of frontal cirri, terminates about in midline of cell very close to rear end of left marginal row; left marginal row begins left of proximal portion of adoral zone.

Length of dorsal bristles not mentioned in original description; according to Fig. 105f about 4 µm. Kinety 1 slightly shortened anteriorly, extends more or less longitudinally to rear cell end with posterior end curved leftwards. Kinety 2 commences at anterior cell end, extends along right body margin, slightly shortened posteriorly in specimen illustrated (Fig. 105f). Caudal cirri lacking.

Specimens of Japanese population studied by Eigner & Foissner (1993) about 90 × 30 µm in life (Fig. 105i, j, Table 32). Body outline elliptical, right body margin slightly concave, left convex and somewhat indented behind adoral zone; posterior portion slightly narrowed, both ends broadly rounded. Contractile vacuole in midbody and near left cell margin, during diastole with collecting canals. Cortical granules lacking, as in type population (see remarks). Cytoplasm with many colourless, fatty shining globules 1–3 µm across. Adoral zone occupies about 35% of body length, bases of membranelles about 7 µm wide in life. Buccal lip extends lid-like across buccal cavity. Undulating membranes as in type population. All cirri about 10 µm long. Buccal cirri in line with middle frontal cirrus and parabuccal cirri in line with right frontal cirrus. A second short frontoventral row right of parabuccal row –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present in 64% of specimens of type population – is lacking (Fig. 105i, j). Rightmost (long) frontoventral row begins right of distal end of adoral zone, extends to cell centre. Transverse cirri lacking. Right marginal row commencing on level of fourth to sixth cirrus of rightmost frontoventral row, curved leftwards posteriorly and terminating near end of left marginal row. Dorsal bristles about 3 µm long in life, arranged in two kineties. Caudal cirri absent.

Body size of Korean specimens studied by Shin (1994, 1998) 90–150 × 35–60 µm (Fig. 105u–w, Table 32). Body very soft and flexible; ventral surface flattened and slightly concave, dorsal side convex. Body outline elongate and rectangular, both ends slightly blunt and broadly rounded. Contractile vacuole spherical; collecting canals neither mentioned nor illustrated. Cytoplasm filled with crystals and 31–50 greasily shining globules. Movement rapid, changing direction frequently. Adoral zone occupies about 32% of body length. Pharyngeal fibres 15–23 µm long (mean = 17.7 µm, n = 10), extend to near right cell margin. Usually only one short frontoventral row between parabuccal row and rightmost (long) frontoventral row[1]. Transverse cirri lacking. Dorsal bristles about 4 µm long, some of them slightly shorter, some slightly longer. Dorsal kinety 1 composed of 15–20 bristles, rear portion composed of three cilia curved leftwards. Caudal cirri absent.

Resting cyst (Fig. 105d): Eigner & Foissner (1991) observed encystment in a clone. Before cyst formation two specimens unite along their oral areas and the rear body portion attenuates. Pairs stop moving and round up, still united along the oral apparatus. Subsequently they separate by slow movement of their cirri which ultimately disappear. Resting cysts usually situated in pairs. Individual cysts spherical to slightly ellipsoidal, 15–42 µm across (38 µm on average, n = 30) , filled with greasily shining globules; wall about 1 µm thick.

Cell division (Fig. 105j–t): Morphogenesis is described in detail by Eigner & Foissner (1993; for review, see Foissner 1996, p. 107). A schematic summary of this process is provided by Eigner (1997).

Morphogenesis commences obviously de novo with the formation of an oral primordium near the end of the marginal rows (Fig. 105j, k). Somewhat later this primordium extends between the rear end of the adoral zone and the posterior cell end. Simultaneously, the parabuccal cirri modify to anlage III for both filial products (Fig. 105l). Subsequently, the buccal row disaggregates to form anlage II of both fil-

← **Fig. 105l–q** *Orthoamphisiella stramenticola* (from Eigner & Foissner 1993. Infraciliature of ventral side after protargol impregnation. l–n, p, q, Austrian population; o, Japanese population. Parental structure white, new black). **l, m:** Early dividers, l = 86 µm, m = 83 µm. **n, o:** Primordium formation in long, rightmost frontoventral row. **p, q:** Middle and middle to late divider, p = 72 µm, q = 69 µm. Arrow in (p) marks splitting of primary primordium in long, rightmost frontoventral row. Short arrows in (q) denote short frontoventral rows of proter; long arrow marks rear end of long, rightmost frontoventral row of proter. II, III = frontal-ventral cirri anlagen II (forms middle frontal cirrus and buccal cirri) and III (forms right frontal cirrus and parabuccal cirri). Page 628.

[1] Rightmost (long) frontoventral row incorrectly designated as "row of midventral cirri" by Shin (1994). The term midventral should be confined to rows with zigzagging cirri (for details, see Berger 2006).

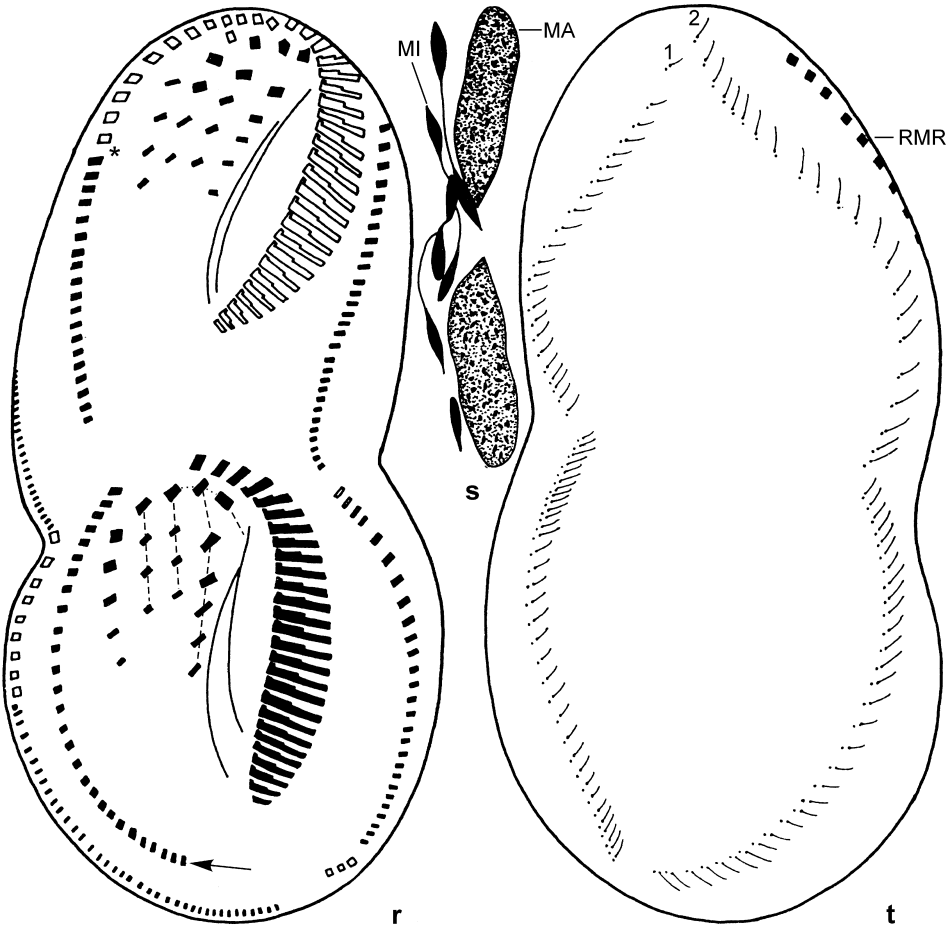


Fig. 105r–t *Orthoamphisiella stramenticola* (from Eigner & Foissner 1993. Austrian population. Protargol impregnation. Parental structures white, new black). **r, s:** Infraciliature of ventral side and nuclear apparatus in dorsal view of late divider, r = 86 µm (nuclear apparatus not drawn to scale). Frontal cirri of opisthe connected by dotted line. Broken lines connect cirri which originate from the same anlage (only shown for anlagen I–IV). Asterisk denotes border between old (anterior) and new (posterior) cirri of long, rightmost frontoventral row of proter. Arrow marks rear end of long, rightmost frontoventral row of opisthe. **t:** Infraciliature of dorsal side of late divider, 84 µm. MA = macronucleus, MI = micronucleus, RMR = right marginal row, 1, 2 = dorsal kineties. Page 628.

ial products (Fig. 105m). The (rearmost) cirri of the other short frontoventral rows are modified to anlagen IV and V (when two short frontoventral rows are present between the parabuccal row and the long frontoventral row) at the same time.

Anlage I of the opisthe is separated from the oral primordium and forms the undulating membranes and the left frontal cirrus of the opisthe (Fig. 105p). It is the sole frontoventral anlage which does not originate via a primary primordium. The anlagen/primary primordia II–V formed in the (parental) frontal field split; the an-

terior portions become the anlagen for the proter, the posterior ones those for the opisthe (Fig. 105p, q). In the middle portion of the parental rightmost (long) frontoventral row an anlage is formed. The division of this anlage occurred slightly earlier in the Austrian population than in the Japanese one (Fig. 105n–p). At this stage, in total six frontoventral anlagen are recognisable, provided that two short rows are formed between the parabuccal row and the long frontoventral row. Specimens with only one short row right of the parabuccal row have only five anlagen; it is not known which anlage (IV or V) is lacking in such specimens. The parental undulating membranes are reorganised, whereas the old adoral zone is retained for the proter.

The rightmost anlage in the opisthe produces 28 cirri in the specimen illustrated (Fig. 105r); all rearmost parental cirri have been disaggregated and involved in this anlage, that is, the rightmost (long) frontoventral row of the opisthe consists of new cirri only. By contrast, only 19 (mean = 19.3, n = 6) cirri are formed in the proter whereas the anteriormost 11 parental cirri (mean = 11.6, n = 18) remain or are "renewed" (likely this means reorganised; see remarks at genus section) in the postdividers (Fig. 105r).

Within each parental marginal row two anlagen are formed, one for the proter and one for the opisthe (Fig. 105q, r). The dorsal kineties divide by intrakinetal proliferation (Fig. 105t; type 1 according to Foissner & Adam 1983a; *Gonostomum* pattern according to Berger 1999, p. 73). No caudal cirri are formed at the end of the new dorsal kineties. In addition, no dorsomarginal kineties originate from/near the new right marginal rows.

The nuclear apparatus divides as usual, that is, the four macronuclear nodules fuse to a single mass. This mass subsequently makes successive amitotic divisions to produce the species specific number of nodules. The micronuclei divide mitotically (Fig. 105j, q, t).

Occurrence and ecology: Terrestrial. The type locality of *O. stramenticola* is the village of Schrötten (46°47'N 15°49'E; altitude 320 m), Styria, Austria, where Eigner & Foissner (1991) discovered it in the leaf litter of a walnut tree (*Juglans*) next to an old farmhouse with the number 22. The meadow under the tree was mowed twice a year and was rich in flora. The top leaves of at least three layers of dry walnut leaves were taken and put into a petri dish and a raw culture was made (Foissner 1987a). A clone was established in Volvic-yeast medium and cultured at 14–22° C (Eigner & Foissner 1991). The sample containing the Austrian population studied by Eigner & Foissner (1993) was collected from the type locality in July 1991. The Japanese population is from near the peak of the "Female" Tsukuba mountain in Japan (altitude about 800 m; collected on 15.07.1989), where Eigner & Foissner (1993) discovered *O. stramenticola* in a sample containing litter and roots from small bamboo and beech trees. Shin (1994, p. 259, station 32; 1998) found it in a moss-covered soil and grassland in Namhansansong (127°10'10"E 37°20'50"N) in Kwangju-gun, South Korea. Further records: two floodplain soils (Müllerboden [Pruno-Fraxinetum], 48°00'N 16°42'E; Beugenau [Fraxino-Populetum]; 48°08'N

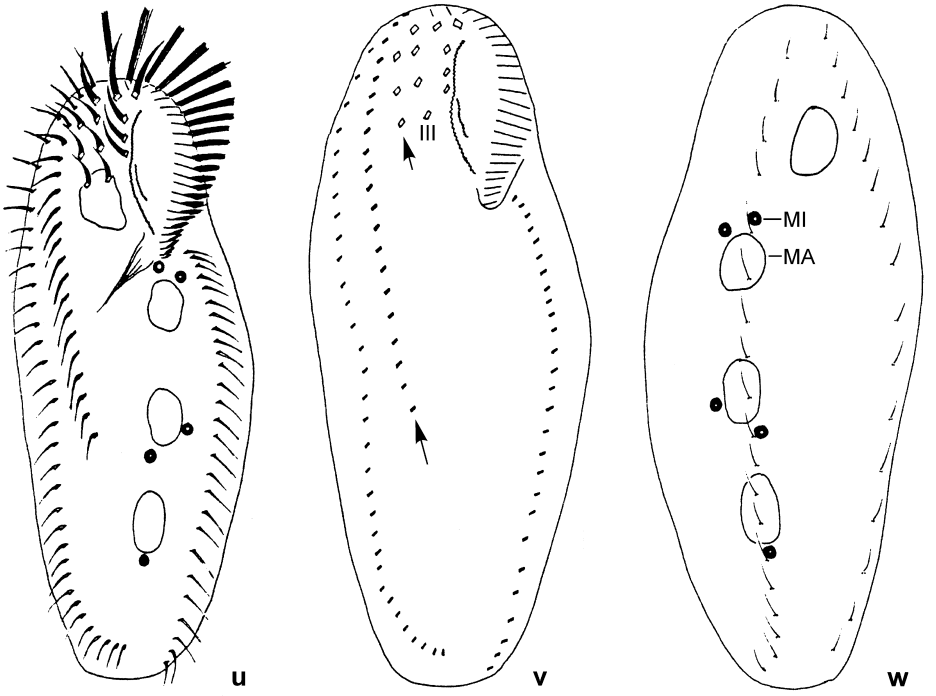


Fig. 105u–w *Orthoamphisiella stramenticola* (from Shin 1994. u, from life; v, w, protargol impregnation). **u:** Ventral view, 90–150 µm (according to the incorrect scale bar the specimen is 195 µm long). **v, w:** Infraciliature of ventral and dorsal side and nuclear apparatus of same(?) specimen (scale bar incorrect). Short arrow marks short frontoventral row, long arrow denotes long, rightmost frontoventral row. MA = macronuclear nodule, MI = micronucleus, III = cirral row (right frontal cirrus and parabuccal cirri) originating from anlage III. Page 628.

16°33'E; both sites calcaric fluvisol, typical mull, recent clay) south-east of the city of Vienna, Austria (Foissner et al. 2005, p. 629); soil sample (upper 2–3 cm fresh and fermented litter layer [mainly from popular, beech, acacia], mosses from the soil surface, and the upper 3–4 cm black moder; pH 5.2) from a reclaimed, opencast coal mining area near the city of Görlitz, Germany, collected on 24.03.1998, that is, about 30 years after reclamation (Foissner 2000a, p. 259); soil and roots from 0–3 cm (pH 4.7; sample 30) and litter and soil from 0–5 cm (pH 4.7; sample 31) from a cloud rain forest near the summit of Monteverde Preserve, Costa Rica (Foissner 1997, p. 323).

Orthoamphisiella stramenticola feeds on colpodid ciliates and possibly also on bacteria (Eigner & Foissner 1991); food vacuoles of Japanese specimens contained fungal spores and filamentous and coccal (about 4 × 3 µm) cyanobacteria (Eigner & Foissner 1993), while Korean specimens ingested ciliates and testate amoeba (Shin 1994). Biomass of 10^6 specimens about 60 mg (Foissner 1998, p. 206).

Orthoamphisiella grelli Eigner & Foissner, 1993
(Fig. 106a–d, Table 32)

1993 ***Orthoamphisiella grelli* nov. spec.**[1] – Eigner & Foissner, Arch. Protistenk., 143: 342, Fig. 13–16, Table 1 (Fig. 106a–d; original description; the holotype slide [accession number 1993/111] is deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Aescht 2008, p. 158; see nomenclature).

2001 ***Orthoamphisiella grelli* Eigner and Foissner, 1993** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 50 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: Eigner & Foissner (1993) dedicated this species to Karl G. Grell, Tübingen, Germany (e.g., Grell 1968). Eigner & Foissner (1993) wrote that one holotype slide and one paratype slide have been deposited in the museum in Linz. According to Aescht (2008, p. 158), the paratype slide is not labelled as such; instead, seven further marked slides have been deposited, five of which with dividing specimens (accession numbers 1993/112–118; Aescht 2003, p. 387).

Remarks: So far, *Orthoamphisiella grelli* is only recorded from an island in the southern hemisphere. Thus, it cannot be excluded that it is endemic. It differs from *O. stramenticola* mainly in the number of macronuclear nodules (usually two against usually four) and buccal cirri (usually two against usually 3–5). According to the original description, minor differences occur in the location of the buccal cirri. However, this impression is obviously mainly due to the different number of buccal cirri. In addition, *Orthoamphisiella grelli* is somewhat smaller than the type species (Table 32).

According to Eigner (1999, p. 46), the present species clusters together with *O. stramenticola*, *Orthoamphisiella franzi* (= *Neowallackia franzi* in present book; p. 281), and *Trachelochaeta gonostomoida* Hemberger, 1985 (= *Gonostomum gonostomoidum*, p. 158). Further details on this topic, see chapter "Foundation for the nonuse of the Orthoamphisiellidae" (p. 626).

Morphology: Body size 60–90 × 20–30 µm in life. Body outline long-elliptical, right margin straight to slightly concave, left one more or less convex; anterior and posterior body portion slightly tapered. Body dorsoventrally inconspicuously flattened; highly flexible (Fig. 106a, b). On average two ellipsoidal macronuclear nodules left of cell midline; individual nodules about 15 × 6 µm in life. Usually 2–3 micronuclei attached to macronuclear nodules, in life about 3 µm across. Contractile vacuole near left cell margin about in mid-body; during diastole with an indistinct anterior and posterior collecting canal. Cortical granules and cytoplasmic crystals lacking. Cytoplasm with some fatty shining globules 2–4 µm across and many food vacuoles 4–7 µm in diameter. Movement not mentioned, indicating that it is inconspicuous.

[1] Eigner & Foissner (1993) provided the following diagnosis: Size in vivo 60–90 × 20–30 µm. 2 macronuclear segments, 20 adoral membranelles, 2 buccal cirri at anterior end of endoral membrane and 7 fronto-ventral cirri in 2–3 short rows on average.

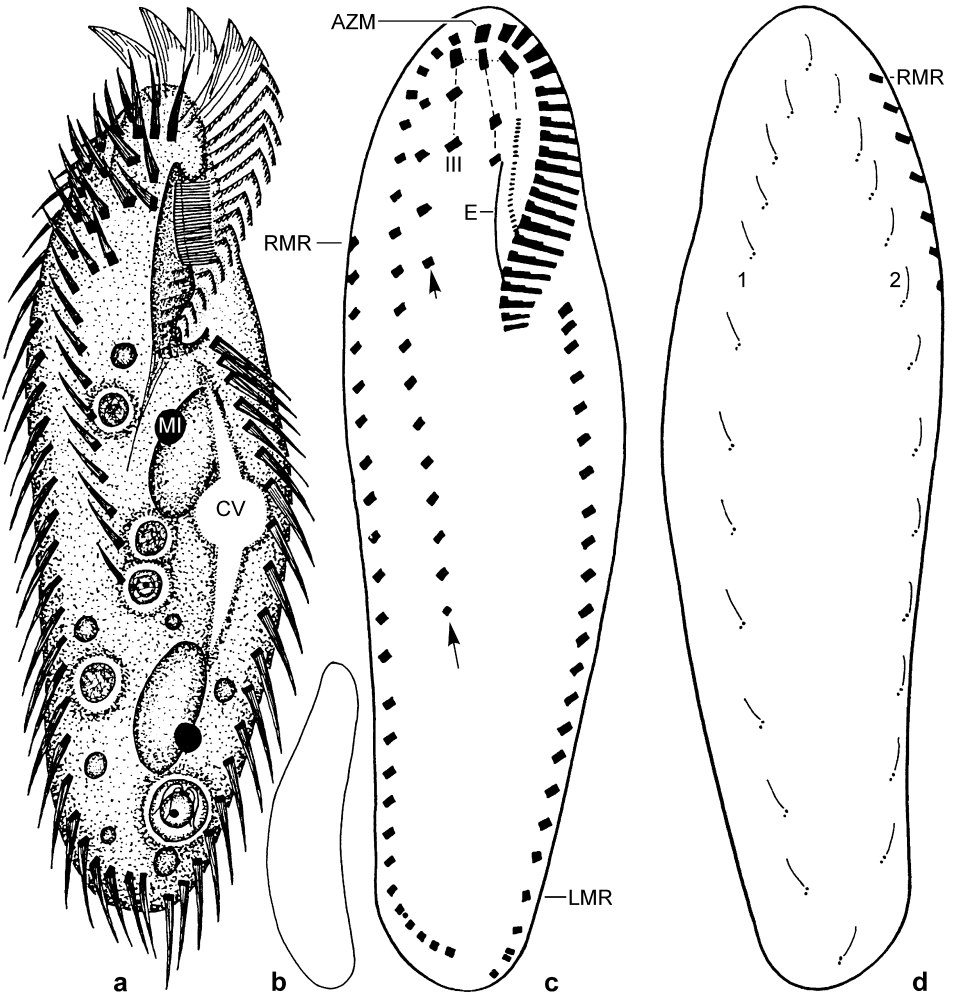


Fig. 106a–d *Orthoamphisiella grelli* (from Eigner & Foissner 1993. a, b, from life; c, d, protargol impregnation). **a:** Ventral view of representative specimen, 80 µm. **b:** Right lateral view showing dorsoventral flattening. **c, d:** Infraciliature of ventral and dorsal side of same(?) specimen, 80 µm. Long arrow marks long frontoventral row, short arrow denotes short row between parabuccal row and long frontoventral row. AZM = distal end of adoral zone of membranelles, CV = contractile vacuole with collecting canals, E = endoral, LMR = left marginal row, MI = micronucleus, RMR = right marginal row, III = cirri (right frontal cirrus and parabuccal cirri) originating from anlage III, 1, 2 = dorsal kineties. Page 639.

Adoral zone of membranelles occupies about 30% of body length (33% on average in protargol preparations; Table 32), composed of 20 membranelles of ordinary fine structure on average; more or less distinctly formed likely a question mark with distal end about in midline, that is, ahead of middle frontal cirrus (Fig. 106c). Buccal lip lid-like, covers right and proximal portion of buccal cavity. Undulating mem-

branes arranged in parallel, that is, do not intersect optically. Paroral straight inserted in shallow fold on oblique left margin of buccal lip, commences about at level of anteriormost buccal cirrus; obviously composed of dikinetids. Endoral slightly curved, runs on right side of buccal cavity; commences about at level of second buccal cirrus. Pharyngeal fibres obviously without peculiarities (Fig. 106a).

Cirral pattern basically as in type species, including variability of short frontoventral cirral rows (Fig. 106c). All cirri about 10 µm long. Frontal cirri more or less distinctly enlarged, form transverse pseudorow immediately behind distal end of adoral zone. Usually two buccal cirri right of anterior portion of paroral. Usually two parabuccal cirri (termed fronto-ventral 1 in original description) behind right frontal cirrus. Short frontoventral row (fronto-ventral row 2 in original description) adjacent to parabuccal row composed of three (range 2–4) cirri on average; row terminates at 26% of body length in specimen illustrated (Fig. 106c). Ten out of 25 specimens measured with an additional short frontoventral row (fronto-ventral row 3 in original description) composed of three cirri on average. Rightmost (long) frontoventral row begins right of distal end of adoral zone, terminates at 60% of body length and composed of 18 cirri on average (Table 32). Postperistomial, pretransverse ventral, and transverse cirri lacking. Right marginal row commences about at level of frontal cirri on dorsolateral surface, distinctly curved leftwards posteriorly and regularly terminating slightly more anteriorly than left marginal row. Left marginal row commences left of proximal portion of adoral zone, extends to near rear cell end.

Dorsal cilia in life 3 µm long, arranged in two more or less bipolar kineties, one left and one right of midline (Fig. 106d). Caudal cirri lacking.

Cell division: This part of the life cycle was studied by Eigner & Foissner (1993; for review Foissner 1996, p. 107). Accordingly, it proceeds very similar as in the type species (*O. stramenticola*) and therefore it was not documented by Eigner & Foissner (1993). However, the primordium for the long, rightmost frontoventral row develops more anteriad, leaving only 3–7 (mean = 4.5; n = 6) parental cirri intact. In contrast, the type species has this primordium in the centre of the row so that 9–14 (mean = 11.6; n = 18) parental cirri remain or are renewed in post-dividers (Fig. 105r).

Occurrence and ecology: Terrestrial. Type locality of *Orthoamphisiella grelli* is the Transvaal Bay (10°00'W 40°20'S) on Gough Island, where it was discovered in a sample of moss and soil (pH 4.3) collected from a river bank (about 50 m altitude) by J. Cooper (South Africa) on October 21, 1990. According to Foissner (1996, p. 285), it occurred also on the Tafelkop, a mountain on this island, namely in moss and mire vegetation (pH 4.5, altitude 500 m) and a pure mire vegetation with very few soil particles (pH 4.5, altitude 500 m). No further records published so far, perhaps because it is an endemic species.

Orthoamphisiella grelli feeds on bacteria and heterotrophic flagellates (Eigner & Foissner 1993). Biomass of 10^6 specimens about 20 mg (Foissner 1998, p. 206).

Incertae sedis in *Orthoamphisiella*

Orthoamphisiella breviseries Foissner, Agatha & Berger, 2002 (Fig. 107a–k, Table 32)

2002 ***Orthoamphisiella breviseries* nov. spec.**[1] – Foissner, Agatha & Berger, Denisia, 5: 703, Fig. 156a–k, 389a–d, Table 139 (Fig. 106a–k; original description; the holotype slide [accession number 2202/114] and two paratype slides [2002/115, 2002/116] are deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; Aescht 2003, p. 382; 2008, p. 147).

2004 ***Orthoamphisiella breviseries* Foissner et al., 2002** – Foissner, Moon-van der Staay, van der Staay, Hackstein, Krautgartner & Berger, Europ. J. Protistol., 40: 267, Fig. 5 (analysis of small subunit ribosomal RNA gene sequence of a Namibian population; NCBI GenBank accession number AY 498654; see nomenclature).

Nomenclature: The species-group name *breviseries* (short-rowed) is a composite of *brev·is*, *-is*, *-e* (Latin adjective; short, small, low), the thematic vowel *·i-*, and *series* (Latin noun; row), referring to the short rightmost frontoventral row (Foissner et al. 2002a). Incorrect subsequent spellings: *Orthoamphisiella breviseris* (Schmidt et al. 2007, p. 203); *Orthamphisiella breviseris* (Sonntag et al. 2008, p. 284).

Remarks: The ventral and dorsal infraciliature (more than one buccal cirrus; postoral ventral and transverse cirri lacking; two dorsal kineties, caudal cirri lacking) of this species is strongly reminiscent of those of the other two *Orthoamphisiella* species, except that a long frontoventral row is lacking in *O. breviseries*. In spite of this difference, we preliminary assigned it to *Orthoamphisiella*. However, simultaneously we stated that it has to be separated at subgeneric or generic level, when ontogenetic data reveal substantial differences (Foissner et al. 2002a). For relationships estimated from molecular data, see section "Molecular data" below and *Gonostomum namibiense* (p. 140).

As just mentioned, *Orthoamphisiella breviseries* differs from *O. stramenticola* and *O. grelli* mainly by the lack of the rightmost, long frontoventral row. In addition, the macronucleus of *O. stramenticola* and *O. grelli* is composed of four, respectively, two distinct nodules, whereas it is a single, more or less dumb-bell-shaped mass in *O. breviseries*. This curiosity separates it also from species of *Afroamphisiella* Foissner et al., 2002a, which have four (*A. abdita*) or 18 (*A. multinucleata*) macronuclear nodules (for review of *Afroamphisiella*, see Berger 2008, p. 371).

In life, *Orthoamphisiella breviseries* is easily identified by the following combination of features (Foissner et al. 2002a): rod-shaped macronuclear mass; few frontoventral cirri (including buccal and parabuccal cirri) arranged in three or four short,

[1] Foissner et al. (2002a) provided the following diagnosis: Size about 100 × 15 µm in vivo, that is, conspicuously elongate ellipsoidal. Macronucleus vermiform to dumb-bell-shaped. 20 adoral membranelles, 2 buccal cirri at anterior end of undulating membranes, and 8 frontoventral cirri in 2 short rows on average. 2 dorsal kineties.

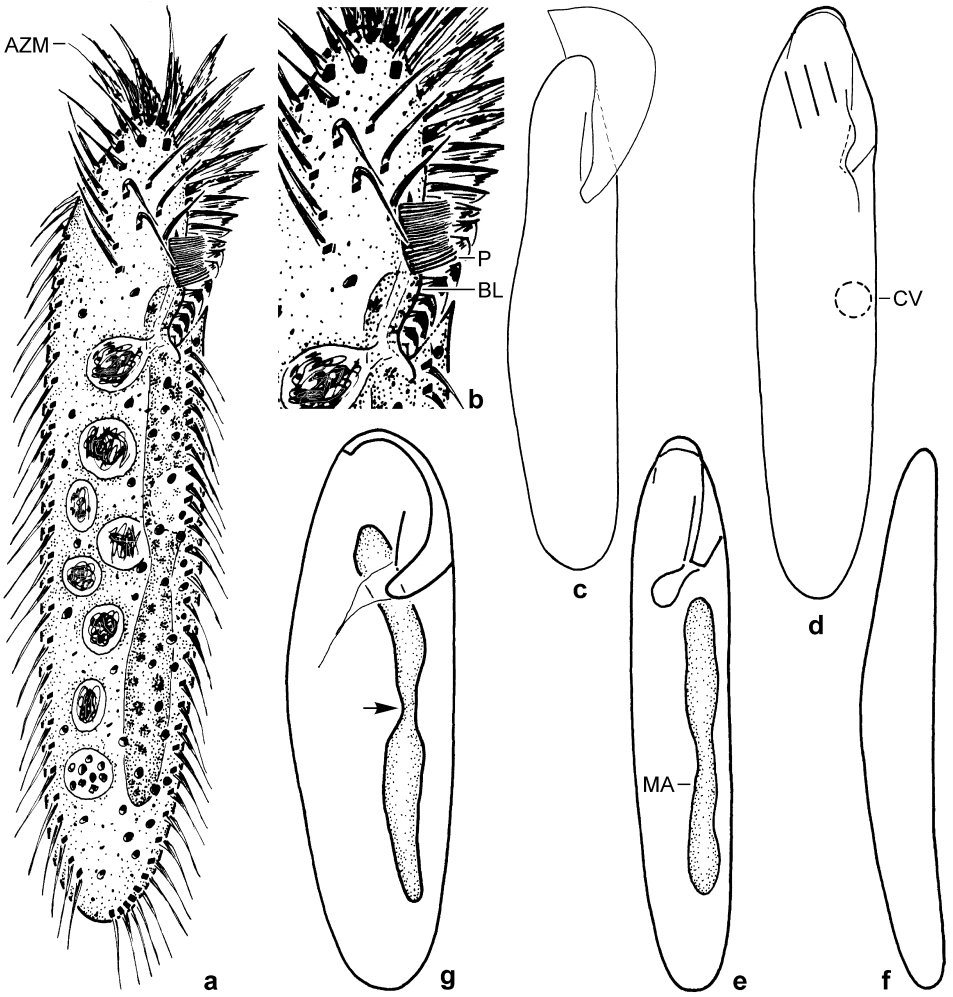


Fig. 107a–g *Orthoamphisiella breviseries* (from Foissner et al. 2002a. a–f, from life; g, protargol impregnation). **a, b:** Ventral view of representative specimen and detail of oral apparatus, 86 µm. **c:** Outline of a freely motile specimen, drawn from video records. **d:** Outline showing oral apparatus and oblique cirral rows. **e:** Outline showing macronucleus and oral apparatus with a forming food vacuole. **f:** Right lateral view showing dorsoventral flattening. **g:** Specimen with slightly constricted macronucleus (arrow). AZM = distal end of adoral zone of membranelles, BL = buccal lip, CV = contractile vacuole, MA = macronucleus, P = paroral. Page 642.

oblique rows not extending beyond level of rear end of the short adoral zone; very flat and narrow buccal cavity.

Morphology: Body size 80–120 × 15–20 µm, usually around 100 × 15 µm in life; length:width ratio about 5.0–6.5:1 in life, 2.5–4.0:1, on average 3.3:1 in protargol preparations, where specimens shrink longitudinally by up to 50%; width, in

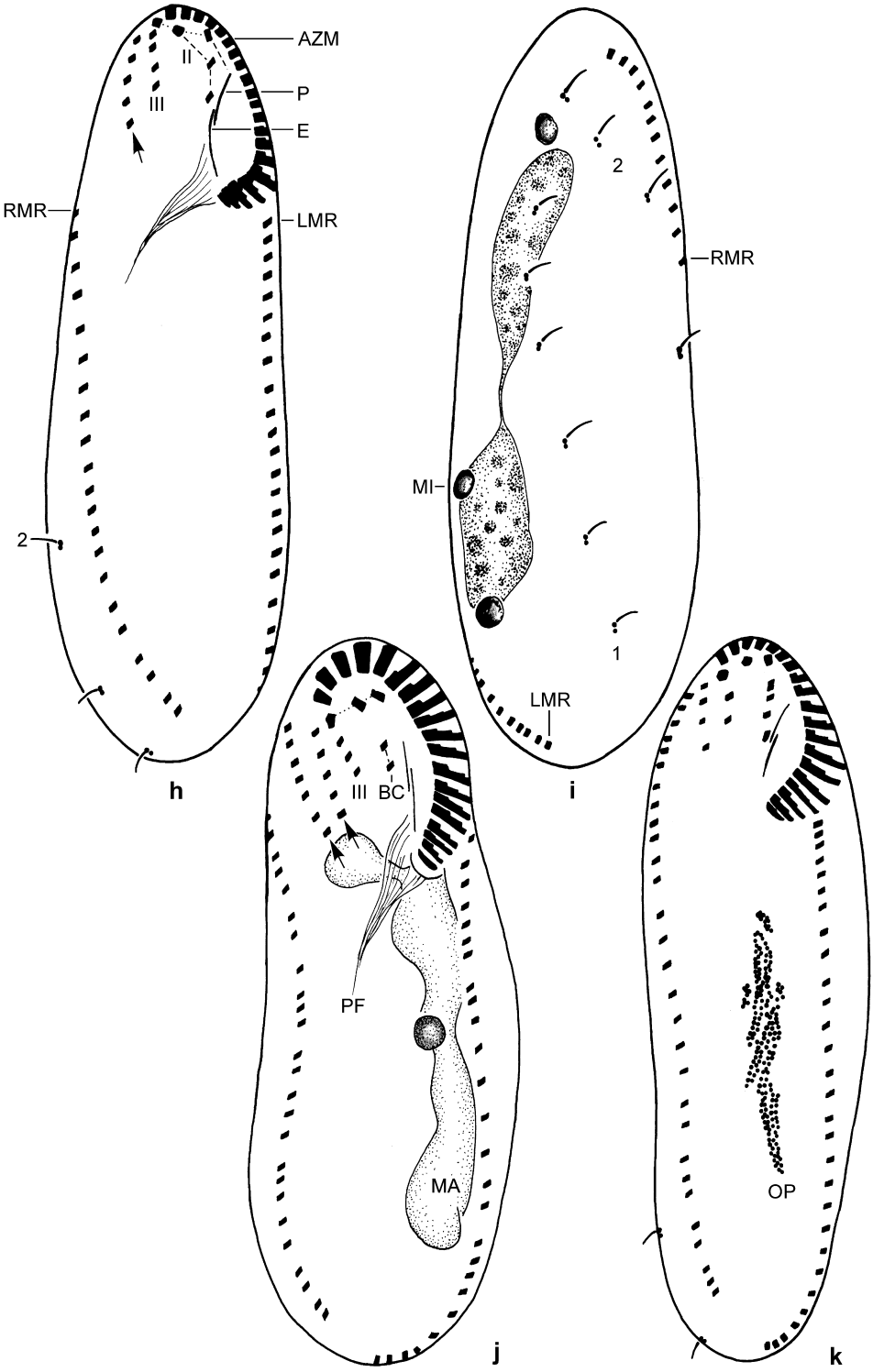
contrast, not changed significantly (Fig. 107a, f, h, Table 32). Body outline elongate, overall shape elliptical to slightly lanceolate with broadest site at buccal entrance, margins straight to slightly convex, ends rounded. Body dorsoventrally flattened up to 2:1, ventral side flat, dorsal slightly vaulted; very flexible, but acontractile. Macronucleus in longitudinal axis of cell left of midline, very likely basically composed of two elongate nodules connected by an unusually broad bridge providing the nucleus with a dumb-bell-shaped or vermiform, wrinkled outline; chromatin bodies 1–3 µm across. Micronuclei globular, attached to or arranged near macronucleus (Fig. 107a, e, g, i, j). Contractile vacuole near mid-body at left cell margin, disappears rapidly under cover glass pressure (Fig. 107a, d). No special cortical granules. Cytoplasm colourless, granulated by lipid droplets 1–2 µm across concentrated at left body margin; without crystals. Food vacuoles slightly ellipsoidal and globular, 5–7 µm across. Movement without peculiarities.

Adoral zone roughly in *Gonostomum* pattern, that is, commences slightly right of midline, extends straight along left body margin, and performs rather abrupt right bend to plunge into buccal cavity (Fig. 107b, g, h, k); conspicuously short, that is, occupies only about 25% of body length in life and 28% on average in shrunken, protargol-impregnated specimens (Table 32); composed of 20 membranelles of usual fine structure on average; largest membranelles 4–5 µm wide in life. Buccal cavity very flat and narrow in life, often broadened in protargol preparations. Buccal lip rather small than large, but conspicuously convex, covers buccal cavity and right half of rear end of adoral zone, bears paroral at upper left margin.[1] Exact arrangement and structure of undulating membranes not known because of preparation artefacts mentioned above; paroral and endoral of about same length, paroral composed of closely spaced, 7 µm long cilia, commences ahead of level of endoral (Fig. 107b, h). Pharyngeal fibres recognisable in life and protargol preparations, extend obliquely backwards.

Cirral pattern very constant, number of cirri of usual variability (Fig. 107h, Table 32). All cirri about 10 µm long in life. Three slightly enlarged frontal cirri in somewhat oblique pseudorow, right cirrus close to distal end of adoral zone. Usually two

Fig. 107h–k *Orthoamphisiella breviseries* (from Foissner et al. 2002a. Protargol impregnation). **h, i:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 48 µm. Frontal cirri connected by dotted line; cirri originating from same anlage connected by broken line (only shown for anlagen I and II). Arrow marks rear end of frontoventral row. **j:** Ventral side of a specimen with two frontoventral rows (arrows), 50 µm. Frontal cirri connected by dotted line. **k:** Ventral side of an early divider, 52 µm. Note that the oral primordium is formed de novo, that is, without any contact to the parental ciliature. AZM = adoral zone of membranelles, BC = buccal cirri, E = endoral, LMR = left marginal row, MA = macronucleus, MI = micronucleus, OP = oral primordium, P = paroral, PF = pharyngeal fibres, RMR = right marginal row, II = cirral row (middle frontal cirrus and two buccal cirri) formed by anlage II, III = cirral row (right frontal cirrus and parabuccal cirri) formed by anlage III, 1, 2 = dorsal kineties. Page 642. →

[1] The population documented by Foissner et al. (2002a) on page 1309 (their Fig. 389a–d) is not the type population. It has only one buccal cirrus and might thus be a distinct (sub)species. In addition, the paroral is at the base of the buccal lip in this population (see also Foissner & AL-Rasheid 2006, p. 11).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buccal cirri right of anterior end of undulating membranes; usually not in line with middle frontal cirrus, which originates from same anlage. Three parabuccal cirri (termed frontoventral row 1 in original description) in line with right frontal cirrus. Rightmost frontoventral row (frontoventral row 2 in original description) with five cirri on average, usually terminates distinctly ahead of level of proximal end of adoral zone. Three of 25 specimens with a second frontoventral row right of the parabuccal row (Fig. 107j). Long frontoventral row and postperistomial, pretransverse, and transverse cirri lacking. Right marginal row commences dorsolaterally near anterior cell end, extends ventrally and terminates subterminally. Left marginal row commences left of proximal end of adoral zone, rear portion J-shaped curved rightwards with narrowly spaced cirri, ending about in midline; marginal rows thus distinctly separated posteriorly.

Dorsal bristles 3–4 µm long in life and very widely spaced (10 µm), arranged in two slightly oblique kineties (Fig. 107h, i, Table 32): kinety 1 distinctly shortened at both ends, extends in midline; kinety 2 roughly bipolar, commences near midline and extends onto right dorsolateral surface posteriorly. Caudal cirri lacking.

Cell division: Foissner et al. (2002a) found only an early divider. Accordingly, morphogenesis commences apokinetally in mid-body (Fig. 107k).

Molecular data: The complete 18S rRNA gene sequence of *Orthoamphisiella breviseries* is 1773 nucleotides long (NCBI GenBank accession number AY498654; Foissner et al. 2004, Berger et al. 2004). It is considered in the analyses by Foissner et al. (2004), Gong et al. (2006, 2007), Schmidt et al. (2007), Shao et al. (2007), Foissner & Stoeck (2008), Sonntag et al. (2008), and Yi et al. (2009). In the trees provided by Foissner et al. (2004) and Shao et al. (2007, p. 262), it clusters together with *Gonostomum namibiense* and *G. strenuum*. The sister group to this cluster is composed of (((*Onychodromopsis flexilis* + *Oxytricha granulifera*) + *Halteria grandinella*) + (*Engelmanniella mobilis* + *Hemiurosoma terricola*)). The tree published by Gong et al. (2006, p. 71) is very similar, with *Trachelostyla pediculiformis* next to the *Orthoamphisiella* + *Gonostomum* group. By contrast, in the trees provided by Gong et al. (2007, p. 475) and Foissner & Stoeck (2006a, p. 262; 2008, p. 16), *Orthoamphisiella breviseries* and *Gonostomum* spp. are rather distinctly separated. According to Schmidt et al. (2007, their Fig. 2) and Sonntag et al. (2008, p. 284), the present species and *Amphisiella magnigranulosa* (= *Uroleptoides magnigranulosus* in the review by Berger 2008, p. 273) are closely related to the urostyloids. The rather different hypotheses show that it is impossible to find the more or less exact phylogenetic position of the present species with this molecular marker. In spite of this great uncertainty, the molecular results basically support the idea derived from morphological data that *O. breviseries* is a non-dorsomarginalian hypotrich. Since its morphological classification in *Orthoamphisiella* is rather uncertain (see remarks), the "molecular" position of *Orthoamphisiella* remains unknown for the time being because no gene sequence data are available for the type species *O. stramenticola*.

Occurrence and ecology: Terrestrial. Type locality of *Orthoamphisiella breviseries* is the margin of the Etosha Pan (19°10'S 15°55'E), Namibia, where Foissner et

al. (2002a) discovered it in a highly saline soil (yellow, sandy loam; pH 9.0; 40‰ salinity) from a sedge stand on a limestone plate about 10 cm under soil surface; litter from soil surface, sedge roots, and soil up to 10 cm have been used (sample collected on 01 Mar 1994; further details, see Foissner et al. 2002a, p. 28, site 61). The scanning electron micrographs provided by Foissner et al. (2002a, p. 1309) are from a population also collected from a highly saline soil from the northern Namib Desert in January 2001 (see footnote in morphology section for important note). In addition, we found it in a highly saline soil sample from Saudi Arabia, indicating that *O. breviseries* prefers saline inland soils (Foissner et al. 2002a). The population from which the 18S rRNA gene sequence was analysed was isolated from a mud and soil sample collected at a water hole in the Etosha (Fischer) Pan, Namibia (Foissner et al. 2004, p. 267). *Orthoamphisiella breviseries* feeds on bacteria (Foissner et al. 2002a).

Saudithrix Foissner, AL-Rasheid & Berger in Berger, AL-Rasheid & Foissner, 2006

2006 ***Saudithrix* Foissner, AL-Rasheid and Berger n. gen.**[1] – Berger, AL-Rasheid & Foissner, J. Euk. Microbiol., 53: 267 (original description). Type species (by original designation): *Saudithrix terricola* Foissner, AL-Rasheid & Berger in Berger, AL-Rasheid & Foissner, 2006.

2008 ***Saudithrix* Berger, AL-Rasheid & Foissner, 2006** – Lynn, Ciliated protozoa, p. 362 (family revision of ciliates).

Nomenclature: Composite of *Saudi* (from Saudi Arabia) and the Greek noun *thrix* (hair = ciliate s. l.), meaning "a ciliate from Saudi Arabia". Feminine gender (Berger et al. 2006b).

Characterisation (A = supposed apomorphy): Non-dorsomarginalian Hypotricha with flexible body ventrally covered by cirral rows originating from intrakinetal anlagen. Oral apparatus *Cyrtohymena*-like with conspicuous, sickle-shaped buccal lip. Frontal ciliature multicoronar (A?). Transverse cirri present. Frontoterminal lacking (A?). Three dorsal kineties. Dorsomarginal kineties and dorsal kinety fragmentation lacking. Caudal cirri absent (A?).[2]

Remarks: See single species.

Species included in *Saudithrix*: (1) *Saudithrix terricola* Foissner, AL-Rasheid & Berger in Berger, AL-Rasheid & Foissner, 2006 (type species).

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[1] Berger et al. (2006b) provided the following diagnosis: Stichotrichia with flexible body ventrally covered by cirral rows originating from intrakinetal anlagen. Oral apparatus cyrtohymenid-like with conspicuous, sickle-shaped buccal lip. Frontal ciliature multicoronar. Transverse cirri present, frontoterminal and caudal cirri absent.

[2] We did not include the number of marginal cirral rows, although an important feature for the characterisation of supraspecific taxa (e.g., Berger 1999, Lynn & Small 2002) in the diagnosis because of the problems described in the morphology section.

Single species

Saudithrix terricola Foissner, AL-Rasheid & Berger in Berger, AL-Rasheid & Foissner, 2006.

(Fig. 108a–z, Table 33)

2006 ***Saudithrix terricola*** – Foissner & AL-Rasheid, Acta Protozool., 45: 2, Fig. 28–30 (description of oral apparatus).

2006 ***Saudithrix terricola*** **Foissner, AL-Rasheid and Berger n. sp.**[1] – Berger, AL-Rasheid & Foissner, J. Euk. Microbiol., 53: 267, Fig. 1–26, Table 1 (Fig. 108a–z; original description; the holotype slide [accession number: 2005/77] and 5 paratype slides [2005/78–82] have been deposited in the Oberösterreichische Landesmuseum in Linz [LI], Upper Austria; see also Aescht 2008, p. 183).

2006 ***Saudithrix terricola*** – Green & Bohannan, Trends in Ecology and Evolution, 21: 505, Fig. 3b (Fig. 108s; discussion of "flagship" species).

2006 ***Saudithrix terricola*** – Chao, Li, Agatha & Foissner, Oikos, 114: 481, Fig. 1 (Fig. 108s; statistical approach to estimate soil ciliate diversity).

2008 ***Saudithrix terricola*** – Cotterill, AL-Rasheid & Foissner, Biodiversity and Conservation, 17: 430, Fig. 1 (Fig. 108s; paper on conservation of protists).

Nomenclature: The species-group name *terricola* (Latin; living in soil) refers to the habitat where the species was discovered (Berger et al. 2006b). Type species of *Saudithrix*.

Remarks: The classification of *Saudithrix* is rather difficult (Berger et al. 2006a, b), although *S. terricola* is very conspicuous due to the large size, the high number of cirri (>440; Table 33) covering the ventral side, and the *Cyrtohymena*-like oral apparatus. Berger et al. (2006b) did not assign it to a certain suprageneric taxon because specific features are lacking, for example, the fragmenting dorsal kinety of the oxytrichids (Berger 1999), the dorsomarginal kinety of the dorsomarginalians (Berger 2006a), or the zigzagging cirral pairs (midventral pattern) of the urostyloids (Berger 2006a, Borror & Wicklow 1983, Lynn & Small 2002). The lack of the urostyloid midventral pattern in *S. terricola* indicates that the reorganisation of the adoral zone of membranelles in *Saudithrix* (Fig. 108y) and the urostyloids, where this feature is common (Berger 2006a), evolved convergently.

The cirral pattern and some ontogenetic traits of *Saudithrix* are reminiscent of *Pseudokahliella* (p. 662; Foissner et al. 1982), *Wallackia* (p. 206; Foissner et al. 2002a), and *Parastrongylidium* (Aescht & Foissner 1992, Fleury & Fryd-Versavel 1984), because the cirral anlagen are formed side by side and largely within the parental rows. However, the narrow and flat buccal cavity and the short undulating membranes of *Pseudokahliella*, *Wallackia*, and *Parastrongylidium* are distinctly dif-

[1] Berger et al. (2006b) provided the following diagnosis: Size about 270 × 100 µm. Elongate ellipsoidal to indistinctly reniform. Two macronuclear nodules. Adoral zone forms a three-quarter circle, usually composed of 59 membranelles occupying about one third of body length. On average two buccal cirri, three frontal rows, eight frontal-ventral rows (including right marginal row[s]), six to nine subterminal transverse cirri, and one left marginal row. Cortical granules lacking. Three dorsal kineties and scattered parental bristles mainly between anterior portion of rows 1 and 2.

Table 33 Morphometric data on *Saudithrix terricola* (from Berger et al. 2006b)

Characteristics [a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	241.3	239.0	34.9	6.5	14.5	184.0	312.0	29
Body, width	92.3	88.0	19.5	3.6	21.1	61.0	136.0	29
Body length:width, ratio	2.7	2.6	0.6	0.1	22.5	1.7	4.3	29
Adoral zone of membranelles, length 1 [b]	69.4	69.0	6.1	1.1	8.8	58.0	80.0	29
Adoral zone of membranelles, length 2 [b]	38.3	38.0	8.3	1.5	21.7	22.0	54.0	29
Body length:length 1 of adoral zone, ratio	3.5	3.5	0.4	0.1	11.1	2.8	4.2	29
Widest adoral membranelle, width	16.8	17.0	1.1	0.2	6.4	15.0	19.0	29
Anterior body end to anterior macronuclear nodule, distance	57.1	60.0	9.9	1.8	17.4	40.0	73.0	29
Anterior macronuclear nodule, length	36.0	32.0	9.7	1.8	26.8	24.0	60.0	29
Anterior macronuclear nodule, width	18.4	18.0	2.2	0.4	12.0	14.0	24.0	29
Anterior macronuclear nodule, length:width ratio	2.0	1.9	0.6	0.1	27.8	1.1	3.5	29
Macronuclear nodules, distance in between	38.7	36.0	13.4	2.5	34.6	22.0	80.0	29
Posterior macronuclear nodule, length	45.2	44.0	10.1	1.9	22.2	26.0	64.0	29
Posterior macronuclear nodule, width	16.6	16.0	2.9	0.5	17.7	10.0	22.0	29
Posterior macronuclear nodule, length:width ratio	2.8	2.7	0.8	0.1	28.0	1.2	4.9	29
Anteriormost micronucleus, length	3.6	3.5	0.7	0.2	20.6	2.5	5.0	22
Anteriormost micronucleus, width	3.2	3.0	0.6	0.1	19.4	2.5	5.0	22
Anterior body end to paroral, distance	19.3	20.0	3.1	0.6	15.8	14.0	25.0	29
Anterior body end to endoral, distance	23.6	24.0	4.8	0.9	20.2	17.0	32.0	28
Anterior body end to anterior buccal cirrus, distance	35.0	34.0	5.4	1.0	15.3	28.0	46.0	29
Anterior and posterior buccal cirrus, distance in between [c]	3.1	3.0	1.2	0.2	39.4	1.0	6.0	29
Posterior body end to FV row 1, distance	99.9	96.5	29.7	5.6	29.7	46.0	170.0	28
Posterior body end to FV row 2, distance	57.4	48.0	25.7	4.8	44.7	30.0	122.0	29
Posterior body end to FV row 3, distance	35.4	30.5	15.7	3.0	44.4	18.0	76.0	28
Posterior body end to FV row 4, distance	25.4	23.5	11.0	2.1	43.2	9.0	55.0	28
Posterior body end to FV row 5, distance	17.1	14.5	8.1	1.5	47.3	4.0	36.0	28
Posterior body end to FV row 6, distance	10.6	12.0	5.9	1.1	55.4	0.0	22.0	27
Posterior body end to FV row 7, distance	13.9	8.0	19.8	4.0	142.8	0.0	78.0	25
Posterior body end to FV row 8, distance	15.1	7.0	20.1	5.2	133.1	0.0	68.0	15
Posterior body end to FV row 9, distance	2.5	2.5	2.4	1.2	95.2	0.0	5.0	4
Posterior body end to rearmost transverse cirrus, distance	25.3	24.0	10.5	1.9	41.3	10.0	56.0	29
Macronuclear nodules, number [i]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	29
Micronuclei near anterior macronuclear nodule, number	0.7	1.0	0.7	0.1	94.2	0.0	2.0	25
Micronuclei near posterior macronuclear nodule, number	1.1	1.0	0.9	0.2	78.7	0.0	3.0	25
Adoral membranelles, number	58.5	59.0	3.3	0.6	5.7	53.0	64.0	29
Buccal cirri, number	2.2	2.0	9.4	0.1	17.7	2.0	3.0	29
Frontal rows, number [f]	3.2	3.0	0.8	0.2	25.5	2.0	5.0	29
Frontal row 1, number of cirri [g]	3.1	3.0	0.8	0.1	25.2	1.0	5.0	29
Frontal row 2, number of cirri [g]	3.7	4.0	0.8	0.1	21.0	2.0	5.0	29
Frontal row 3, number of cirri [g]	4.0	4.0	0.8	0.2	19.4	3.0	6.0	23
Frontal row 4, number of cirri [g]	4.8	5.0	1.0	0.3	20.4	3.0	6.0	11
Frontal row 5, number of cirri [g]	5.0	–	–	–	–	–	–	1
Frontoventral rows, number	7.9	8.0	0.7	0.1	8.5	7.0	9.0	29
Frontoventral row 1, number of cirri	26.0	28.0	6.2	1.1	23.6	8.0	35.0	29

Table 33 Continued

Characteristics [a]	Mean	M	SD	SE	CV	Min	Max	n
Frontoventral row 2, number of cirri	37.6	37.0	5.0	0.9	13.3	28.0	46.0	28
Frontoventral row 3, number of cirri	45.3	45.0	5.6	1.1	12.4	31.0	58.0	26
Frontoventral row 4, number of cirri	50.9	51.0	5.3	1.0	10.5	41.0	63.0	27
Frontoventral row 5, number of cirri	52.5	53.0	5.12	1.0	9.6	43.0	64.0	28
Frontoventral row 6, number of cirri	55.0	54.0	8.1	1.6	14.8	43.0	73.0	27
Frontoventral row 7, number of cirri	55.0	54.0	10.6	2.0	19.3	29.0	73.0	27
Frontoventral row 8, number of cirri	58.1	60.0	16.2	3.7	27.8	21.0	82.0	19
Frontoventral row 9, number of cirri	62.6	59.0	10.4	4.6	16.5	53.0	76.0	5
Transverse cirri, number [e]	7.3	7.0	0.8	0.2	11.6	6.0	9.0	29
Transverse cirri, total number [e]	7.5	8.0	0.8	0.2	11.0	6.0	9.0	29
Left marginal row, number of cirri [d]	65.7	65.0	9.5	1.8	14.4	48.0	86.0	29
Total number of cirri [h]	440.6	454.0	76.2	14.1	17.3	159.0	545.0	29
Dorsal kineties, number	3.1	3.0	0.2	0.1	7.3	3.0	4.0	20
Cyst, large diameter in life	87.3	90.0	7.5	1.6	8.6	75.0	100.0	23
Cyst, small diameter in life	84.1	84.0	6.8	1.4	8.1	75.0	100.0	23

[a] All measurements in µm. CV = coefficient of variation in %, FV = frontoventral row, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated (? = sample size not known; if two values are known then they are listed as Min and Max; if only one value is known then it is listed as Mean), SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens unless otherwise indicated.

[b] Length 1 = distance between anterior end of cell and proximal end of adoral zone of membranelles. Length 2 = distance between anterior end of cell and distal end of adoral zone of membranelles (see Fig. 1c in Berger 2006a).

[c] When three buccal cirri are present, then the distance between the anteriormost and middle cirrus was measured.

[d] Cirri right and left of main row not included.

[e] Set off cirrus (Fig. 108p) not included (number), respectively, included (total number).

[f] Cirral rows which do not extend beyond the buccal vertex (cirrus I/1 and buccal cirral row not included; Fig. 108k).

[g] Anteriormost (frontal) cirrus included.

[h] Cirri of short rows left or right of main left marginal row not included.

[i] Very rarely occur specimens with three or four macronuclear nodules (Fig. 108b).

ferent from that of *Saudithrix*, where the buccal cavity is wide and deep and the membranes are long and curved; further, the adoral zone of membranelles is roughly in a *Gonostomum*-like pattern in the former three genera, while a three-quarter circle in *Saudithrix*. This suggests that *Saudithrix* is not closely related to these genera, whose suprageneric position (especially of *Pseudokahliella* and *Parastrongylidium*) is also in discussion (e.g., see present book and Berger et al. 1985, Eigner 1997, Lynn & Small 2002, Shi et al. 1999, Tuffrau & Fleury 1994). Thus, we classified *Saudithrix* as genus incertae sedis in the Stichotrichia (= Hypotricha of the present Monographic Series). The presence of three more or less bipolar kineties (that is,

lack of kinety fragmentation and dorsomarginal rows) indicates that *Saudithrix* branches off outside the Dorsomarginalia. By contrast, the preservation of dorsal kineties is reminiscent of the kahliellid genus *Parakahliella* (p. 397). Very likely, meaningful gene sequence data are needed for a better estimation of the phylogenetic position. Lynn (2008) took over our non-specific classification.

Saudithrix terricola has a unique combination of features and thus we established a new genus (Berger et al. 2006b). The marine *Pseudokahliella* (see p. 662) lacks transverse cirri and has a paroral composed of dikinetids, whereas the terrestrial *Saudithrix* has distinct transverse cirri and a widened paroral. *Anatoliocirrus* Özbek & Foissner in Foissner et al. (2002a, b) has, like *Saudithrix*, a widened paroral, but possesses frontoterminal and caudal cirri and a dorsomarginal kinety, and the frontal-ventral-transverse cirral anlagen originate by transverse division of long primary primordia. By contrast, *Saudithrix* lacks frontoterminal and caudal cirri and a dorsomarginal kinety, and the cirral anlagen of the proter and the opisthe originate independently from each other.

Gigantothrix Foissner, 1999 lacks transverse cirri (vs. present in *Saudithrix*) and has a rigid body (vs. flexible), a long adoral zone (46% vs. 29%), and a complex dorsal ciliature (many kineties due to dorsomarginal rows and multiple kinety fragmentation vs. three bipolar kineties). The latter three features assign *Gigantothrix* unequivocally to the Stylonychinae, as defined by Berger (1999).

The overall appearance of the eye-catching species *Saudithrix terricola* is reminiscent of several large soil hypotrichs with many cirri, for example, *Eschaneustyla lugeri*, *Afrokahliella binucleata*, *Anatoliocirrus capari* (Foissner et al. 2002a, Berger 2006a), and *Gigantothrix herzogi* (Foissner 1999). *Eschaneustyla lugeri* has a very similar frontal ciliature, but possesses, inter alia, 60 macronuclear nodules (vs. two), cortical granules (vs. lacking), three frontoventral rows (including right marginal row vs. eight), four dorsal kineties with caudal cirri (vs. three without caudal cirri), but lacks transverse cirri (vs. present; for review see Berger 2006a). *Afrokahliella binucleata* and *Anatoliocirrus capari* have, like *Saudithrix terricola*, two macronuclear nodules and a rather variable arrangement and number of cirral rows. However, they are distinctly smaller than *S. terricola* (body length 130–140 µm vs. 270 µm), have three frontal cirri and one buccal cirrus (vs. multicorona and two buccal cirri), and four dorsal kineties (including one dorsomarginal kinety) with many caudal cirri (vs. three, and dorsomarginal kinety and caudal cirri lacking). In addition, *Parakahliella binucleata* lacks transverse cirri (vs. present in *S. terricola* and *A. capari*).

The habitus of *Gigantothrix herzogi* Foissner, 1999 is very similar to that of *S. terricola*, especially as concerns body size (250–400 × 120–200 µm) and cirral pattern. However, they can be easily distinguished by the nuclear apparatus (33 macronuclear nodules roughly arranged in C-shaped figure vs. two), the consistency of the body (rigid vs. very flexible), the length of the adoral zone (46% vs. 29%), the transverse cirri (lacking vs. present), and the dorsal ciliature (many kineties due to dorsomarginal rows and multiple kinety fragmentation vs. three bipolar kineties).

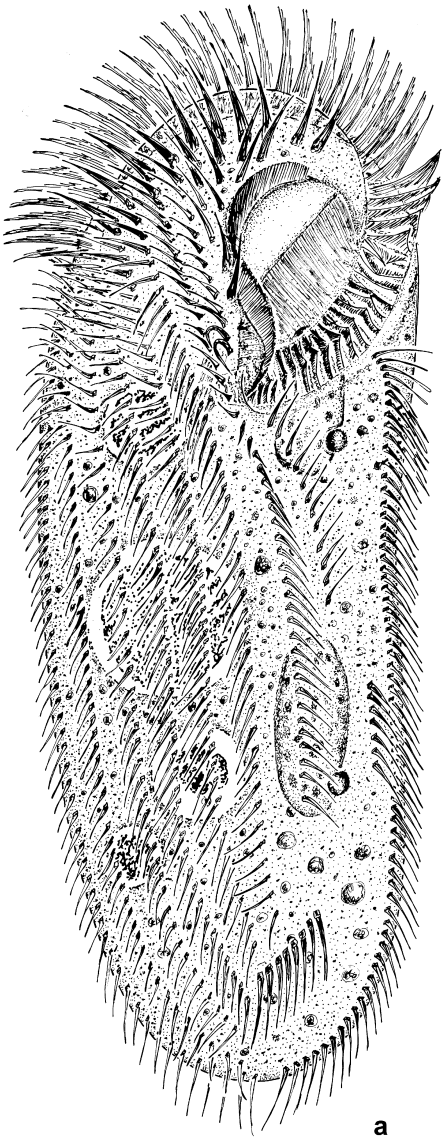
Some limnetic hypotrichs are also reminiscent of *S. terricola*. The common *Urostyla grandis* has, inter alia, many small macronuclear nodules (vs. two), conspicuous cortical granules (vs. lacking), and zigzagging midventral pairs (vs. absent; for review see Berger 2006a, p. 1148). The following species have, like *S. terricola*, only two macronuclear nodules: *Paraurostyla weissei* (for review, see Berger 1999, p. 844) can be easily distinguished from *S. terricola* by the cortical granulation (present vs. lacking), details of the cirral pattern (e.g., three or four frontal cirri and one buccal cirrus vs. multicorona and usually two buccal cirri) and the dorsal ciliature (caudal cirri plus six or seven rows including dorsomarginal rows and kinety fragmentation vs. caudal cirri lacking and three kineties). *Pseudourostyla raikovi* and *P. magna* from freshwater habitats in Azerbaijan are large (about 180 µm) and very large (about 500 µm), respectively, and possess not only many left marginal rows but, more importantly, a midventral complex composed of distinctly zigzagging cirri (for review, see Berger 2006a, p. 807, 809); by contrast, midventral pairs are lacking in *S. terricola*.

The habitus of *Parabirojimia similis*, a marine species, is also similar to that of *S. terricola* (for review, see Berger 2006a, p. 691; Hu et al. 2002). They differ, inter alia, in the number of macronuclear nodules (3–6 vs. two), in the shape of the adoral zone of membranelles (bipartite vs. continuous), and in details of the cirral pattern (three frontal cirri plus some zigzagging midventral cirri vs. multicorona and zigzagging cirri lacking).

In life, *Saudithrix terricola* is best recognised by the following combination of features: body large (200–350 × 70–150 µm) and flexible; two macronuclear nodules; cortical granules lacking; ventral side completely covered by cirri arranged in about nine rows; two buccal cirri on average; many frontal cirri arranged in a multicorona; subterminal transverse cirri; buccal cavity deep, at right bordered by a sickle-shaped lip; terrestrial.

Morphology: Body size 200–350 × 70–150 µm in life, usually near 270 × 100 µm; length:width ratio about 2.7:1 both in life and in protargol preparations (Table 33). Body about 2:1 dorsoventrally flattened, very flexible. Body outline elliptical to elongate elliptical or indistinctly reniform, usually slightly narrowing posteriorly; both ends broadly rounded (Fig. 108a, c, d). Nuclear apparatus left of body midline usually comprising two macronuclear nodules and two micronuclei, specimens with three or four nodules rarely occur; individual nodules bluntly to elongate ellipsoidal, average length:width ratio of anterior nodule 2.0:1, of posterior 2.8:1 (Table 33), contain many small to moderately large, globular chromatin bodies, and often also a

Fig. 108a–e *Saudithrix terricola* (from Berger et al. 2006b. a, c–e, from life; b, protargol impregnation). **a:** → Ventral view of a representative specimen, 267 µm. **b:** Ventral view of a specimen with four macronuclear nodules, 306 µm. **c, d:** Shape variants in dorsal (c; 317 µm) and ventral (d; 219 µm) view showing contractile vacuole system (c) and sickle-shaped buccal lip that ends in a distinct horn distally (d; arrow). **e:** Resting cyst (cyst wall diameter 87 µm) with mucous layer. AZM = adoral zone of membranelles, BL = sickle-shaped buccal lip, CW = cyst wall, MA = macronuclear nodule, MI = micronucleus, ML = mucous layer, P = paroral. Page 648.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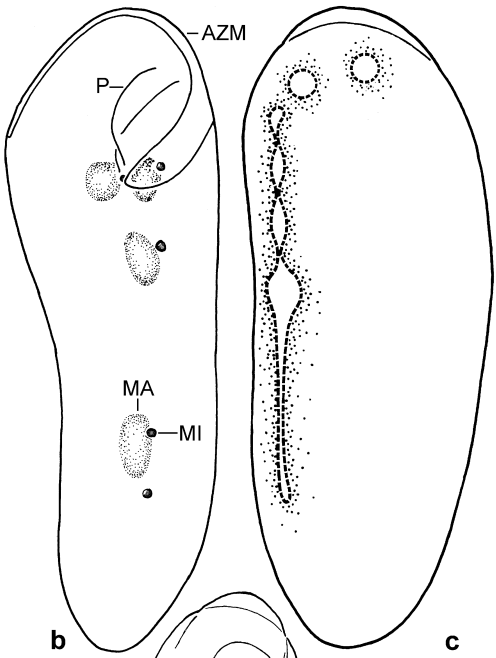
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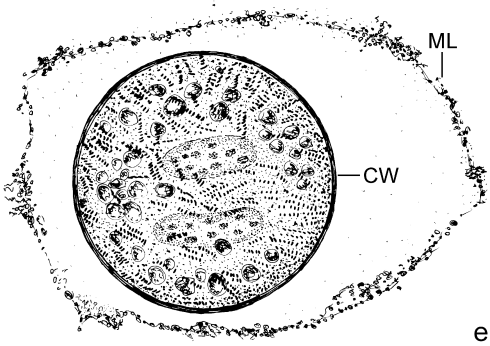
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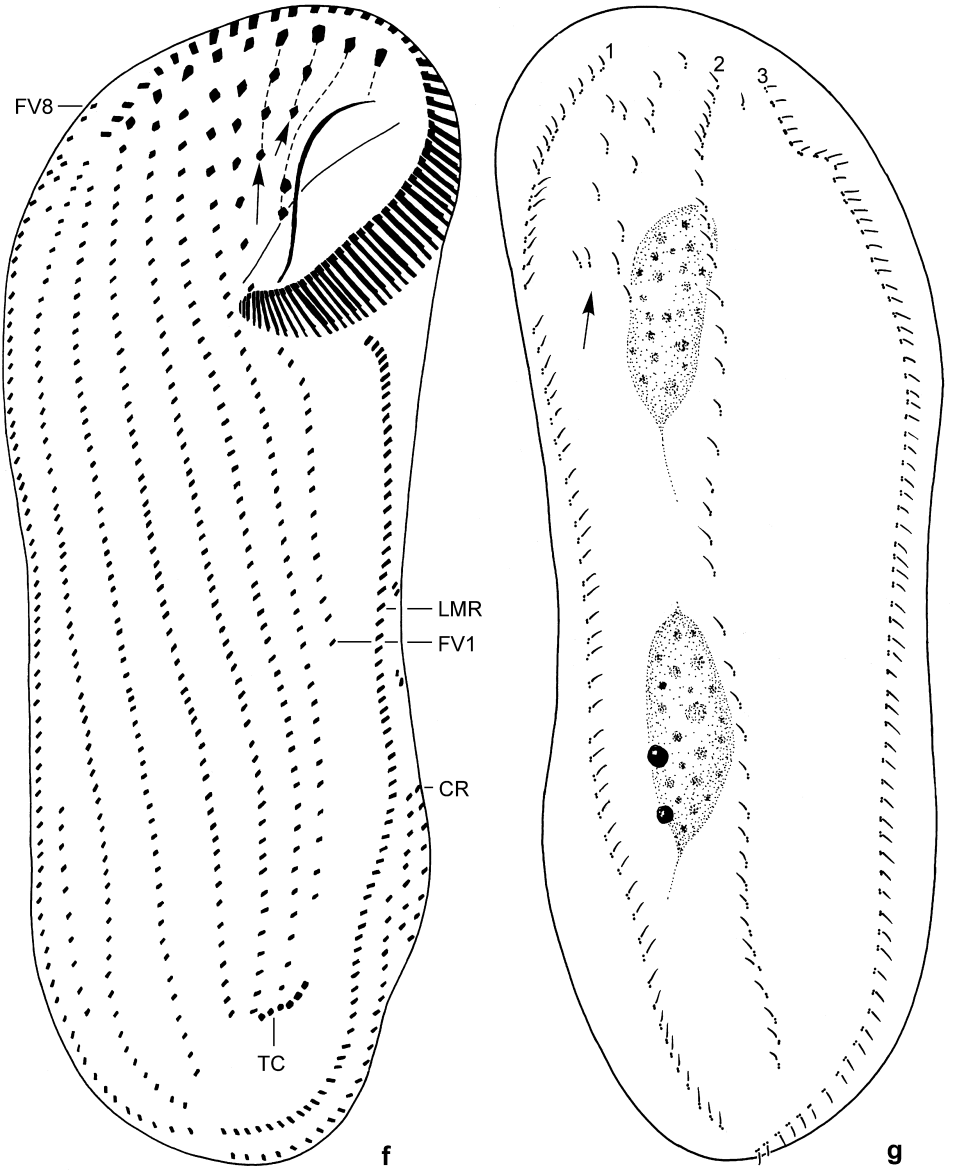
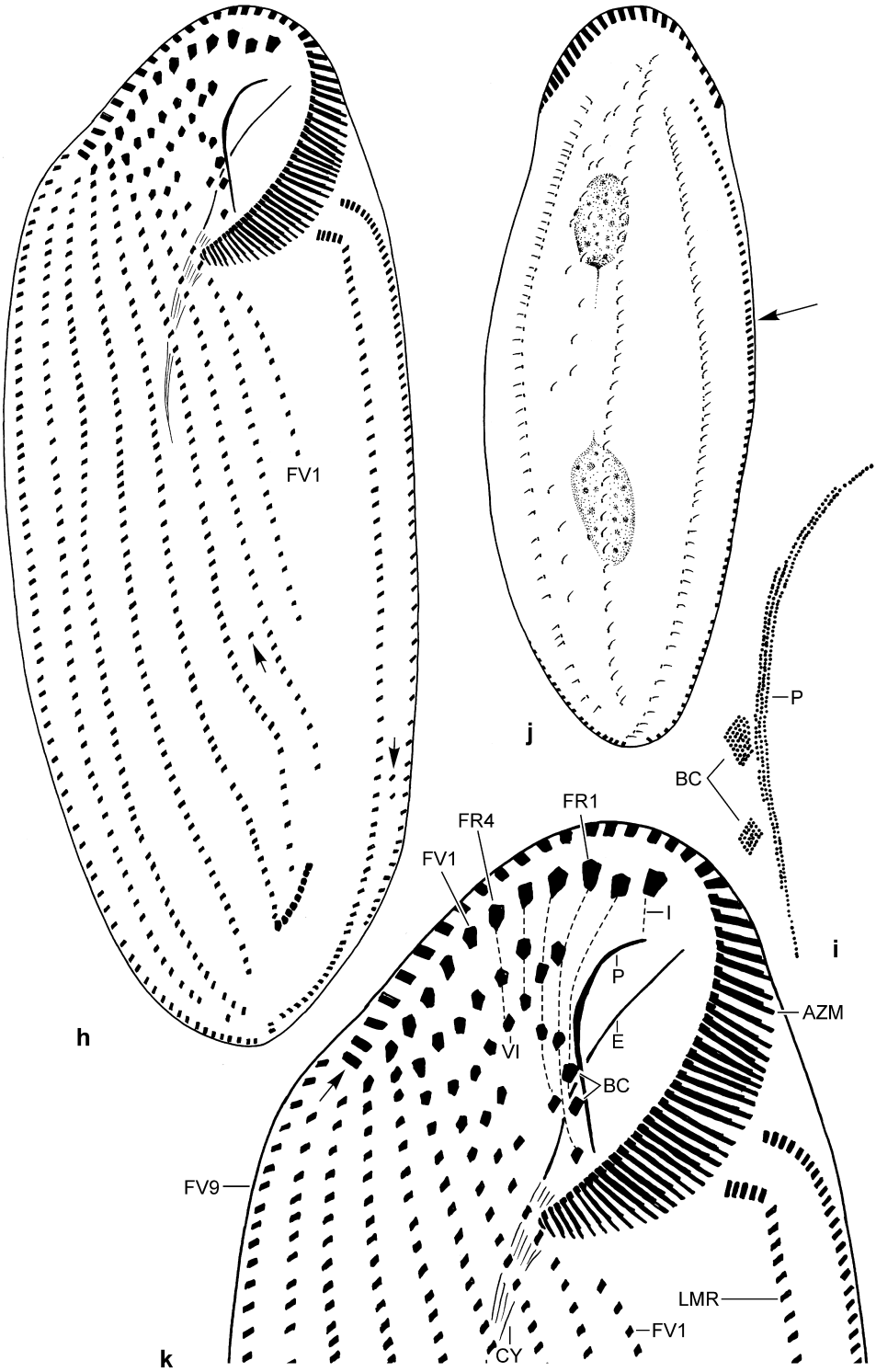


Fig. 108f, g *Saudithrix terricola* (from Berger et al. 2006b. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, 243 µm. Broken lines connect cirri originating from same anlage (shown only for some rows on frontal field, and corresponding transverse cirri not included). Arrows in (f) denote frontal rows 1 (short arrow) and 2 (long arrow). Arrow in (g) marks scattered parental dorsal bristles between the anterior portion of kineties 1 and 2. CR = short cirral rows, FV1, 8 = frontoventral rows, LMR = left marginal row, TC = transverse cirri, 1–3 = dorsal kineties. Page 648.

branched chromatin aggregate. Usually one micronucleus attached to each macronuclear nodule, globular to slightly ellipsoidal, 4–5 µm across in life (Fig. 108a, b, g, j, l, m, o). Contractile vacuole near mid-body at left margin of cell, with two long, lacunar collecting canals and some satellite vacuoles along anterior cell margin during diastole (Fig. 108c). Cortex very soft and flexible, does not contain specific granules. Cytoplasm colourless, contains innumerable granules, rather many lipid droplets, 1–5 µm across, and up to 50 µm-sized food vacuoles. Movement without peculiarities, that is, swims rather rapidly on microscope slide showing great flexibility when crawling between and on soil particles.

Adoral zone occupies 29% of body length on average, composed of an average of 59 membranelles with up to 25 µm-long cilia; bases of largest membranelles about 17 µm wide in life. Proximal portion of adoral zone conspicuously curved rightwards, while distal end extends so far onto right body margin that the zone becomes shaped like a three-quarter circle (Fig. 108a, f, h, k–m, t). Buccal apparatus conspicuous, especially in life, because of the deep cavity and the sickle-shaped lip that forms a distinct process (horn) along the adoral zone. Anterior half of buccal lip semicircular and flat, posterior straight and gradually increasing in height, partially covering proximal part of adoral zone of membranelles (Fig. 108a, d, l, s, t). Buccal cavity covered by an upper and lower seal, that is, delicate membranous structures recognisable only in the scanning electron microscope and described in detail by Foissner & AL-Rasheid (2006). Paroral does not extend along whole buccal lip, but only to summit of sickle-curve; rather wide, except for anterior and posterior end, because composed of short rows comprising up to four basal bodies with about 30 µm-long cilia; length of cilia gradually decreasing to about 15 µm towards ends of membrane. Endoral likely composed of a single row of dikinetids bearing about 10–15 µm long cilia, slightly curved, extends diagonally across dorsal wall of buccal cavity, optically intersecting with paroral near level of buccal cirri, and thus forming a *Cyrtohymena*-pattern (for explanation, see Berger 1999, p. 62). Pharyngeal fibres extend obliquely backwards to about 40% of body length (Fig. 109a, f, h, i, k, m, q, t).

Cirral pattern rather variable, especially the number of frontal, frontoventral, and left marginal rows; cirri 20–25 µm long in life (Table 33). Frontal ciliature of multicorona-type; frontal cirri gradually decrease in size posteriorly; leftmost frontal cirrus (= cirrus I/1) ahead of distal end of paroral. Usually two, rarely three, buccal cirri right of mid-buccal cavity. On average three frontal and eight frontoventral cirral rows, including right marginal row(s) (Fig. 108f, h, k, m, s, Table 33). Leftmost frontoventral row usually with distinct break at level of buccal vertex, terminates on average at 41% of body length; going rightwards, frontoventral rows usually gradually lengthen. Frontoventral rows occasionally with more or less distinct breaks and short extra rows and/or single cirri at variable positions (Fig. 108f, h). Rightmost cirral row usually extends laterally or dorsolaterally, commences near distal end of adoral zone. Left marginal row extends to cell end, anterior portion more or less distinctly curved rightwards and often with very narrowly spaced cirri; frequently, cirral row fragments and/or single cirri right and/or left of main row. Transverse cirri


FV1
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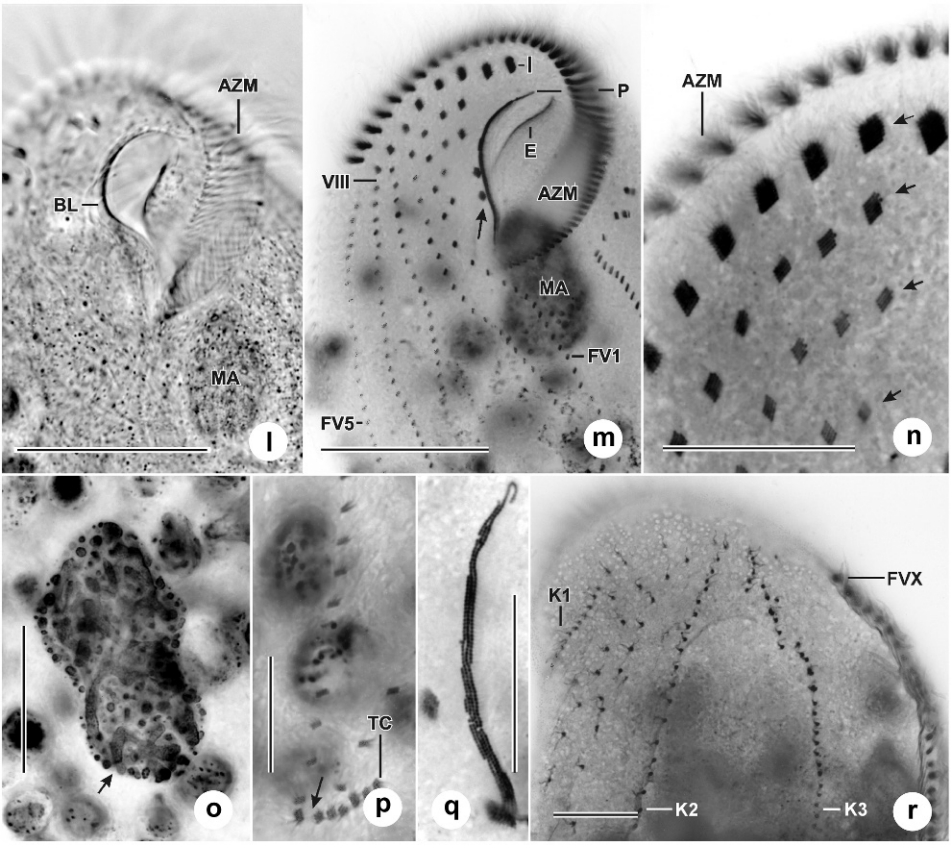

Fig. 108l–r *Saudithrix terricola* (from Berger et al. 2006b. l, from life; m–r, protargol impregnation). **l:** Oral region of a squeezed specimen showing, inter alia, the deep buccal cavity and the sickle-shaped buccal lip. **m:** Infraciliature of ventral side of anterior body third. Arrow marks buccal cirri. **n:** The anterior cirri of the frontal and frontoventral rows become gradually smaller posteriorly and form a multicorona, that is, four or more bows (arrows; note that these bows are pseudorows). **o:** Macronuclear nodule with globular and branched (arrow) chromatin aggregates. **p:** The rightmost transverse cirrus is sometimes slightly separated from the other transverse cirri (arrow). **q:** The middle portion of the paroral is widened and consists of several kinetofragments. **r:** Anterior portion of dorsal infraciliature showing, inter alia, the remnants of the parental kineties between kineties 1 and 2. AZM = adoral zone of membranelles, BL = buccal lip, E = endoral, FV1, 5, X = frontoventral rows 1, 5, X (= outermost right marginal row), K1–3 = dorsal kineties, MA = macronuclear nodule, P = paroral, TC = transverse cirri, I, VIII = cirral anlagen. Scale bars = 50 µm (l, m), 20 µm (n–r). Page 648.

← **Fig. 108h–k** *Saudithrix terricola* (from Berger et al. 2006b. Protargol impregnation). **h, k:** Infraciliature of ventral side of a paratype specimen, 290 µm. Arrows in (h) mark supernumerary cirri between frontoventral rows 3 and 4 and between the main left marginal row (right) and an additional row (left). Arrow in (k) denotes distal end of adoral zone. Broken lines connect cirri which originate from the same anlage (not shown for all rows). **i:** The paroral is widened in the central portion. **j:** Infraciliature of dorsal side and nuclear apparatus of a paratype specimen, 262 µm. Arrow marks rightmost frontoventral row (= outermost right marginal row). Note scattered parental bristles between kineties 1 and 2. AZM = adoral zone, BC = buccal cirri, CR = short cirral rows, CY = cytopharynx, E = endoral, FR1, 4 = frontal rows, FV1, 9 = frontoventral rows, LMR = main left marginal row, P = paroral, TC = transverse cirri, I, VI = cirri anlagen I and VI. Page 648.

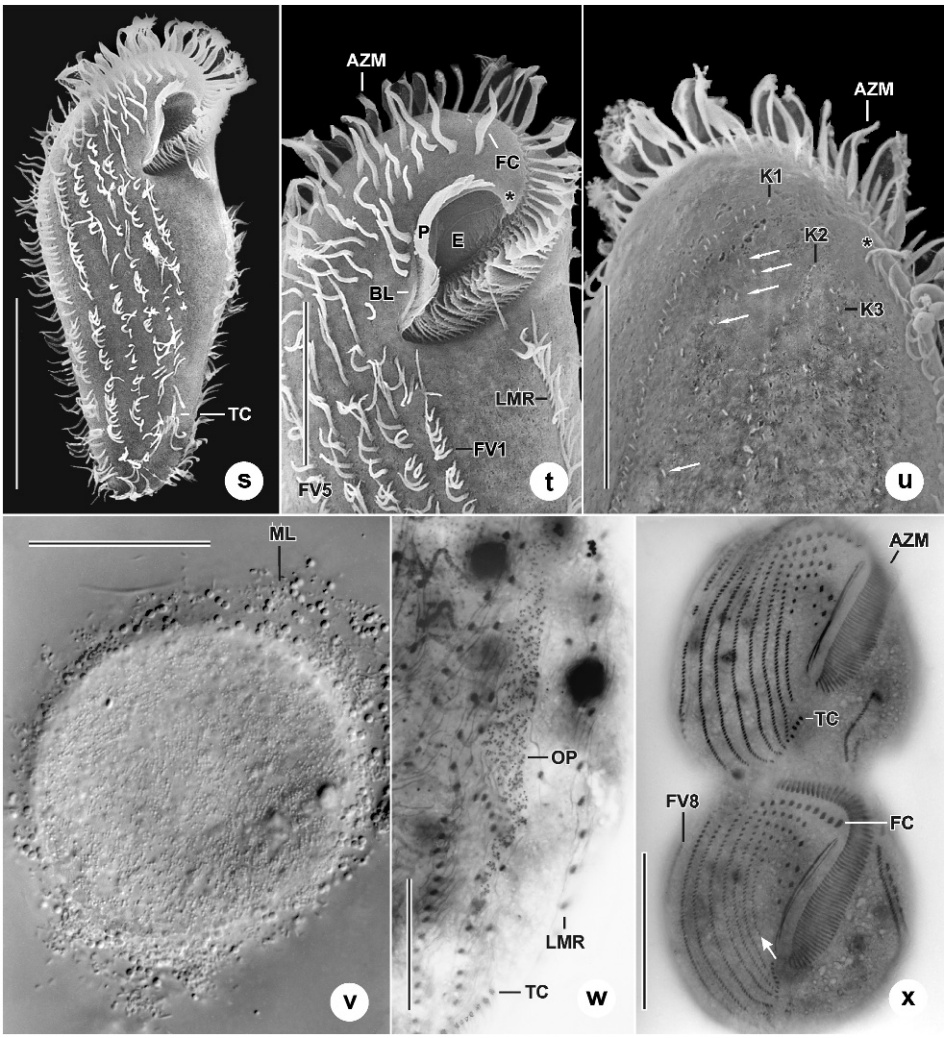

Fig. 108s–x *Saudithrix terricola* (from Berger et al. 2006b. s–u, scanning electron micrographs; v, from life; w, x, protargol impregnation). **s, t:** Overview showing the dense cirral pattern, the almost circular buccal cavity, and the sickle-shaped buccal lip containing the paroral. Note that the paroral does not extend onto the buccal horn (asterisk). **u:** Anterior portion of dorsal side showing the distal adoral membranelles inserting on the frontal scutum. Note the scattered dorsal bristles (arrows), which are remnants from the parental kineties. Asterisk marks anterior end of outermost frontoventral row. **v:** Resting cyst with mucous layer and stripes of ellipsoidal granules underneath cyst wall. **w:** Ontogenesis commences with the formation of an oral primordium left of the posterior portion of the leftmost frontoventral rows. **x:** Ventral view of very late divider (illustrated in Fig. 108z). Arrow marks frontoventral row 1 of the opisthe. AZM = adoral zone of membranelles of proter, BL = buccal lip, E = endoral, FC = leftmost frontal cirrus (= cirrus I/1), FV1, 5, 8 = frontoventral cirral rows, K1–3 = dorsal kineties, LMR = left marginal row, ML = mucous layer, OP = oral primordium, P = paroral, TC = transverse cirri. Scale bars = 100 µm (s, x), 50 µm (t–v), 20 µm (w). Page 648.

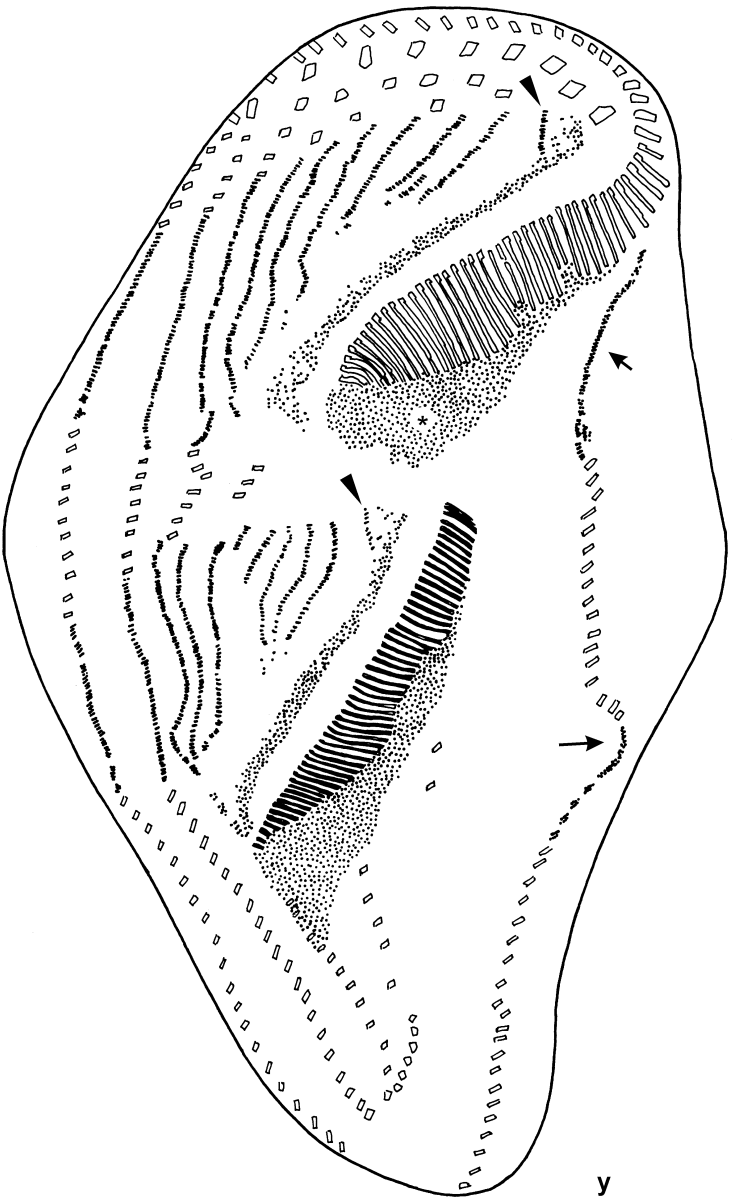

Fig. 108y *Saudithrix terricola* (from Berger et al. 2006b. Protargol impregnation). Ventral view of a middle to late divider, 237 µm. Asterisk marks the reorganising part of the parental adoral zone of membranelles. Arrows denote left marginal row primordia, while arrowheads mark the anlage for the leftmost frontal cirrus. Parental structures white, new black (except for the left-proximal part of the parental adoral zone which is reorganised). Page 648.

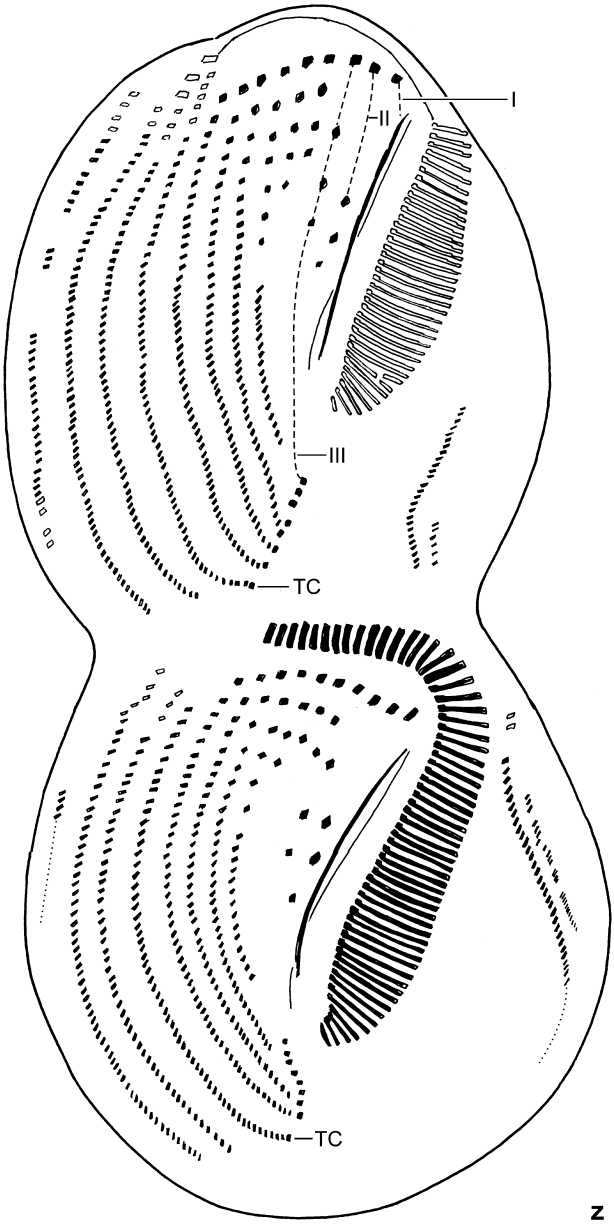

Fig. 108z *Saudithrix terricola* (from Berger et al. 2006b. Protargol impregnation). Ventral view of a very late divider (from Fig. 108x). Broken lines (proter) connect cirri originating from anlagen I–III. Dotted lines mark cirral rows not clearly recognisable in the micrograph (cp. Fig. 108x). Parental structures white, new black (except for the left-proximal part of the parental adoral zone which is reorganised). TC = rightmost transverse cirrus, I–III = leftmost cirral anlagen. Page 648.

subterminal, not projecting beyond rear body end, slightly enlarged and arranged in oblique pseudorow with rightmost cirrus sometimes set off (Fig. 108a, f, h, p, s, Table 33).

Dorsal bristles about 4 µm long in life, basically arranged in three bipolar kineties, but only kinety 3 extends to rear cell end while rows 1 and 2 end subterminally. Anterior end of kinety 3 occasionally with some irregularities. Usually some scattered (parental; see cell division) dikinetids between anterior half of kineties 1 and 2, rarely some pairs also in posterior half and/or between anterior portion of kineties 2 and 3. Caudal cirri lacking (Fig. 108g, j, r, u, Table 33).

Resting cyst: Resting cyst spherical to slightly ellipsoidal, 87 µm in diameter on average, colourless. Cyst wall about 2 µm thick, homogenous, covered by an up to 40 µm thick, mucous layer easily lost when specimens are transferred onto the slide. Cyst content composed of many ellipsoidal granules (1.5 × 1.0 µm) forming stripes underneath wall; many globular and irregular, colourless lipid droplets 4–6 µm in diameter; and two macronuclear nodules (Fig. 108e, v, Table 33).

Cell division: Berger et al. (2006b) found some well-prepared dividers showing the following details (Fig. 108w–z): (i) ontogenesis commences with the formation of an oral primordium left of the posterior portion of the leftmost frontoventral rows extending near to the transverse cirri (Fig. 108w); (ii) the rightmost frontoventral cirral rows, including right marginal row(s), and the left marginal row originate by intrakinetal proliferation (within-row formation; Fig. 108y); (iii) the cirral streaks are arranged roughly side by side (Fig. 108y); (iv) the leftmost frontal cirrus originates, as is usual, from the anlage of the undulating membranes (Fig. 108y, z); (v) the left and the posterior part of the proximal portion of the parental adoral zone are reorganised (Fig. 108y); (vi) the leftmost frontal-ventral row often separates into an anterior and posterior portion, while the other rows usually remain continuous (Fig. 108x, z); (vii) a very late divider and the morphometric analysis show that cirral anlage II, which forms the buccal cirri, does not produce a transverse cirrus (Fig. 108x, z); (viii) the three dorsal kineties develop within the parental rows; (ix) the scattered bristles between dorsal kineties 1 and 2 are remnants of parental rows 1 and 2; (x) likely, dorsomarginal kineties are not formed; (xi) the nuclear apparatus divides in the usual way, that is, the two macronuclear nodules fuse to a single mass in middividers; later, the mass divides to the species-specific pattern.

Occurrence and ecology: *Saudithrix terricola* is likely confined to terrestrial habitats and certainly an eye-catching species[1] because if its enormous size (see

[1] The term flagship species, introduced by conservation biologists, is likely inappropriate for ciliates. According to Caro et al. (2004, p. 64f), a flagship species has been variously defined: (i) A popular charismatic species that serves as a symbol and rallying point to stimulate conservation awareness and action; (ii) a species that draws financial support more easily ... and by so doing serves to protect habitat and other species under the "umbrella" of their large habitat requirements; (iii) a species that has become a symbol and leading element of an entire ecosystem campaign; and (iv) normally a charismatic large vertebrate that can be used to anchor a conservation campaign because it arouses public interest and sympathy. A typical flagship species is the giant panda (*Ailuropoda melanoleuca*). Further reading: Andelman & Fagan (2000), Nentwig et al. (2004, p. 372).

Green & Bohannan 2006 for note on this topic). Type locality of *Saudithrix terricola* is in Adiriyah city (24°45'N 46°33'E) about 20 km north of the capital Riyadh, Saudi Arabia, where we discovered it in a soil sample from a vegetable field (Berger et al. 2006b; Foissner et al. 2008a, p. 321). Also recorded from soil in China (Foissner 2007, p. 6; Foissner et al. 2008, p. 354; Cotterill et al. 2008, p. 430). Berger et al. (2006b) established a culture in Eau de Volvic enriched with some drops of percolate from a non-flooded Petri dish raw culture and a few crushed wheat grains to stimulate growth of bacteria and prey protozoa. Feeds on ciliates (Berger et al. 2006b).

Pseudokahliella Berger, Foissner & Adam, 1985

1985 ***Pseudokahliella* nov. gen.**[1] – Berger, Foissner & Adam, Protistologica, 21: 309 (original description). Type species (by original designation): *Kahliella marina* Foissner, Adam & Foissner, 1982.

1987 ***Pseudokahliella* Berger, Foissner et Adam, 1985** – Tuffrau, Annls Sci. nat. (Zool.), 8: 115 (classification of hypotrichs).

1994 ***Pseudokahliella* Berger et al., 1985** – Tuffrau & Fleury, Traite de Zoologie, 2: 137 (classification of hypotrichs).

2001 ***Pseudokahliella* Berger, Foissner & Adam 1985** – Aescht, Denisia, 1: 136 (catalogue of generic names of ciliates).

2001 ***Pseudokahliella* Berger, Foissner and Adam, 1985** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 76 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).

2002 ***Pseudokahliella* Berger, Foissner and Adam, 1985** – Lynn & Small, Ciliophora, p. 455 (guide to ciliate genera).

2003 ***Pseudokahliella* Berger et al., 1985** – Hu, Gong & Song, Pathogenic ciliates, p. 161 (guide to pathogenic ciliates).

2007 ***Pseudokahliella* Berger, Foissner et Adam, 1985** – Jankowski, Ciliophora, p. 462 (generic revision of ciliates).

2008 ***Pseudokahliella* Berger, Foissner & Adam, 1985** – Lynn, Ciliated protozoa, p. 357 (family revision of ciliates).

2009 ***Pseudokahliella* Berger et al., 1985**[2] – Hu, Warren & Song, Hypotrichs, p. 398 (guide to hypotrichs of Yellow Sea).

Nomenclature: No derivation of the name is given in the original description. *Pseudokahliella* is a composite of *pseud-* (Greek; lie, deception), the thematic vowel *-o-* (in composites at the end of the first root when the second begins with a consonant; Werner 1972), and the genus-group name *Kahliella* (see p. 347 for derivation). The name alludes to the resemblance of *Pseudokahliella marina* and *Kahliella* species. Feminine gender because ending with *-ella* (ICZN 1999, Article 30.1.3).

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[1] Berger et al. (1985) provided the following diagnosis: Kahliellidae with an evolved frontal ciliature and numerous self-replicating somatic ("right marginal") cirral rows.

[2] Hu et al. (2009) provided the following characterisation: Frontal cirri distinctly differentiated. One right and one or two left marginal rows. More than two frontoventral rows. Transverse and caudal cirri not differentiated.

Characterisation (A= supposed apomorphy): Non-dorsomarginalian hypotrich with many self-replicating (right marginal?) cirral rows. Adoral zone of membranelles occupies about 50% of body length. Transverse cirri lacking (A?). Three bipolar dorsal kineties. Dorsomarginal kineties and dorsal kinety fragmentation. Caudal cirri absent (A?). Marine.

Remarks: *Pseudokahliella* was originally classified in the Kahliellidae because of the meridionally arranged cirral rows and the lack of transverse cirri (Berger et al. 1985). This classification was accepted by the founder of the Kahliellidae (Tuffrau 1987, Tuffrau & Fleury 1994), but also by Lynn & Small (2002), Jankowski (2007), and Lynn (2008).

Eigner (1997, p. 558) did not consider the present genus/species in his paper in detail, likely because the cell division was not described in all particulars by Foissner et al. (1982). He supposed that *Pseudokahliella marina* is related to *Parastrongylidium* Fleury & Fryd-Versavel, 1984 and therefore assigned it to the Orthoamphisiellidae Eigner, 1997. *Parastrongylidium* has a little pronounced frontal ciliature sensu stricto and only one dorsal kinety against distinct frontal cirri and three kineties in *Pseudokahliella* (Fleury & Fryd-Versavel 1984, Aescht & Foissner 1992).

Shi et al. (1999, p. 99) and Shi (1999, p. 251, 252) synonymised *Pseudokahliella* with *Kahliella* which, however, has a distinctly lower number of newly formed cirral rows. In addition, *Pseudokahliella* lacks parental cirral rows and a dorsomarginal kinety, both of which are present in *Kahliella*. Later, the Chinese workers accepted *Pseudokahliella* (Hu & Song 2003, Hu et al. 2003, 2009). For further remarks, see single species.

Species included in *Pseudokahliella* (basionym given): (1) *Kahliella marina* Foissner, Adam & Foissner, 1982 (type species).

Single species

Pseudokahliella marina (Foissner, Adam & Foissner, 1982) Berger, Foissner & Adam, 1985

(Fig. 109a–q, 110a–q, Table 34)

1982 ***Kahliella marina* nov. spec.**[1] – Foissner, Adam & Foissner, Protistologica, 18: 218, Abb. 3a–n, 12–17, Tabelle II (Fig. 109a–q; original description; site not mentioned where type slides have been deposited, see nomenclature).

1985 ***Pseudokahliella marina* (Foissner et al., 1982) nov. comb.** – Berger, Foissner & Adam, Protistologica, 21: 309 (combination with *Pseudokahliella*).

[1] Foissner et al. (1982) provided the following diagnosis: In vivo etwa 150–230 × 55–75 µm große, anterior und posterior mäßig bis stark verschmälerte *Kahliella* mit durchschnittlich 10 Makronucleus-Teilen und 12 links schräg verlaufenden Cirrenreihen, die prae-oral zum Teil verkürzt sind, wodurch eine « Naht » entsteht. Frontal- und Marginalcirren deutlich verstärkt. Adorale Membranellenzone zum Teil von einem hyalinen Munddach überdeckt. Durchschnittlich 70 adorale Membranellen, konstant 3 Dorsalkineten. Marin.

2001 ***Pseudokahliella marina* (Foissner, Adam and Foissner, 1982) Berger, Foissner and Adam, 1985** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 41 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs and euplotids).

2002 ***Pseudokahliella marina*** – Lynn & Small, Ciliophora, p. 455, Fig. 44A, B (Fig. 109f, g; guide to ciliate genera).

2003 ***Pseudokahliella marina* (Foissner et al., 1982)** – Hu & Song, J. nat. Hist., 37: 2034, Fig. 1–48, Table 1 (Fig. 110a–q; description of two Chinese populations and cell division; voucher slides likely deposited in the Laboratory of Protozoology, Ocean University of Qingdao, China).

2003 ***Pseudokahliella marina* (Foissner et al., 1982)** – Hu, Gong & Song, Pathogenic ciliates, p. 161, Fig. 5-8G–I (Fig. 110a, g, i; guide to pathogenic ciliates).

2009 ***Pseudokahliella marina* (Foissner et a., 1982) Berger et al., 1985** – Hu, Warren & Song, Hypotrichida, p. 399, Fig. 11.2A, B, 11.14I–K (Fig. 110a, g, i; guide to hypotrichs of Yellow Sea).

Nomenclature: No derivation of the species-group name is given in the original description. The name *marin·us, -a, -um* (Latin adjective [m; f; n]; living in the sea, belonging to the sea) refers to the habitat (Mediterranean Sea) where the species was discovered. Type species of *Pseudokahliella*. Eigner (1997, p. 558) mentioned *Kahliella franzi* as basionym of *Pseudokahliella marina* by mistake. *Parakahliella marina* in Song (2004, p. 748) is likely an unintended combination of *Kahliella marina* with *Parakahliella* Berger, Foissner & Adam, 1985.

The type slides are not deposited in the Oberösterreichische Landesmuseum in Linz (LI), Upper Austria (Aescht 2008, p. 194).

Remarks: Foissner et al. (1982) classified the present species only provisionally in *Kahliella* because the frontoventral ciliature of *K. marina* is also reminiscent of *Paraurostyla* Borror, 1972, especially as concerns the distinct frontal cirri and the more or less well developed marginal rows. However, *Kahliella* and *Paraurostyla* differ, inter alia, in the transverse and caudal ciliature (absent vs. present). Foissner et al. (1982) mentioned a high similarity in the morphogenesis of *Kahliella* and *Paraurostyla* making a clear assignment of the present species impossible. This statement was correct for that time because the morphogenesis of the dorsal ciliature was not known. Now, the separation is very easy because *Paraurostyla* has a fragmenting dorsal kinety proving that it belongs to the oxytrichids (Wirnsberger et al. 1985; for review, see Berger 1999, p. 841). By contrast, a fragmentation is lacking in the kahliellids showing that *Paraurostyla* and *Kahliella* are not closely related.

In 1985, we recognised that *K. marina* should not be classified in *Kahliella* and therefore we established *Pseudokahliella* using the "well-developed" ciliature on the frontal area and the high dominance of the marginal cirral rows as main features (Berger et al. 1985). However, we retained *Pseudokahliella* in the kahliellids, a classification which is very likely incorrect for the following reasons: (i) *Kahliella* has a dorsomarginal kinety, which is lacking in *P. marina*; and (ii) *Kahliella* has parental cirri, a main feature of the kahliellids. By contrast, cirri of the previous generation(s) are absent in *Pseudokahliella*. Especially the lack of a dorsomarginal kinety strongly indicates that *Pseudokahliella* branched off outside the Dorsomarginalia to which *Kahliella* very likely belongs. For that reason, *Pseudokahliella* – with the single species *P. marina* – is classified as non-dorsomarginalian hypotrich.

Table 34 Morphometric data on *Pseudokahliella marina* (ma1, type population from Foissner et al. 1982; ma2, ma3, two populations from Hu & Song 2003)

Characteristics [a]	Population	Mean	M	SD	SE	CV	Min	Max	n
Body, length	ma1	144.2	140.0	24.2	6.0	16.8	112.0	182.0	15
	ma2	147.8	–	13.1	2.9	8.9	127.0	170.0	21
	ma3	133.0	–	29.3	7.3	22.0	102.0	194.0	16
Body, width	ma1	61.7	61.0	5.3	1.4	8.6	53.0	70.0	15
	ma2	90.0	–	8.7	1.9	9.7	72.0	110.0	21
	ma3	84.3	–	34.4	8.6	40.8	56.0	158.0	16
Adoral zone of membranelles, length	ma1	68.3	70.0	8.1	2.1	11.9	56.0	84.0	15
	ma2	81.5	–	9.1	2.1	11.1	68.0	103.0	19
	ma3	64.3	–	16.6	4.2	25.8	52.0	104.0	16
Macronuclear nodule, length	ma1	10.8	9.8	3.9	1.0	35.6	7.0	22.0	15
	ma2	12.2	–	2.0	0.4	16.3	8.0	16.0	20
	ma3	17.8	–	4.7	1.4	26.3	13.0	29.0	12
Macronuclear nodule, width	ma1	7.2	7.0	0.9	0.2	12.5	5.6	9.0	15
	ma2	9.0	–	1.2	0.3	13.8	6.0	11.0	20
	ma3	11.7	–	1.6	0.5	13.8	10.0	14.0	12
Adoral membranelles, number	ma1	66.0	70.0	9.1	2.3	13.8	51.0	76.0	15
	ma2	58.0	–	9.1	2.4	15.7	43.0	68.0	15
	ma3	50.4	–	14.8	3.7	29.3	32.0	83.0	16
Macronuclear nodules, number	ma1	10.5	10.0	2.1	0.5	19.9	8.0	15.0	15
	ma2	16.1	–	2.6	0.6	16.2	10.0	20.0	20
	ma3	12.3	–	2.6	0.9	21.3	9.0	17.0	8
Enlarged frontal cirri, number	ma1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	ma2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	16
	ma3	3.0	3.0	0.0	0.0	0.0	3.0	3.0	16
Right marginal row [b], number of cirri	ma1	41.1	42.0	2.7	0.7	6.6	37.0	46.0	15
	ma2	35.5	–	6.9	1.9	19.4	24.0	47.0	13
	ma3	36.9	–	3.5	0.9	9.5	31.0	43.0	16
Left marginal row, number of cirri	ma1	28.9	29.0	3.6	0.9	12.5	23.0	37.0	15
	ma2	30.8	–	4.4	1.1	14.4	22.0	37.0	15
	ma3	32.8	–	2.9	0.7	8.9	28.0	38.0	16
Cirral rows, number [c]	ma1	12.6	12.0	1.2	0.3	9.9	10.0	15.0	15
	ma2	8.7	–	0.8	0.2	8.6	8.0	10.0	13
	ma3	8.5	–	1.0	0.3	12.2	7.0	10.0	16
Frontoventral row V [d], number of cirri	ma1	32.3	33.0	3.4	0.9	10.4	26.0	38.0	15
Dorsal kineties, number	ma1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	ma2	3.0	–	0.0	0.0	0.0	3.0	3.0	16
	ma3	3.0	–	0.0	0.0	0.0	3.0	3.0	16

[a] All measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum value, mean = arithmetic mean, Min = minimum value, n = number of individuals investigated, SD = standard deviation, SE = standard error of arithmetic mean. Data based on protargol-impregnated specimens.

[b] Outermost right cirral row.

[c] Including marginal rows and short frontoventral rows (anlage I, that is, left frontal cirrus not included).

[d] Leftmost frontoventral row extending beyond buccal vertex.

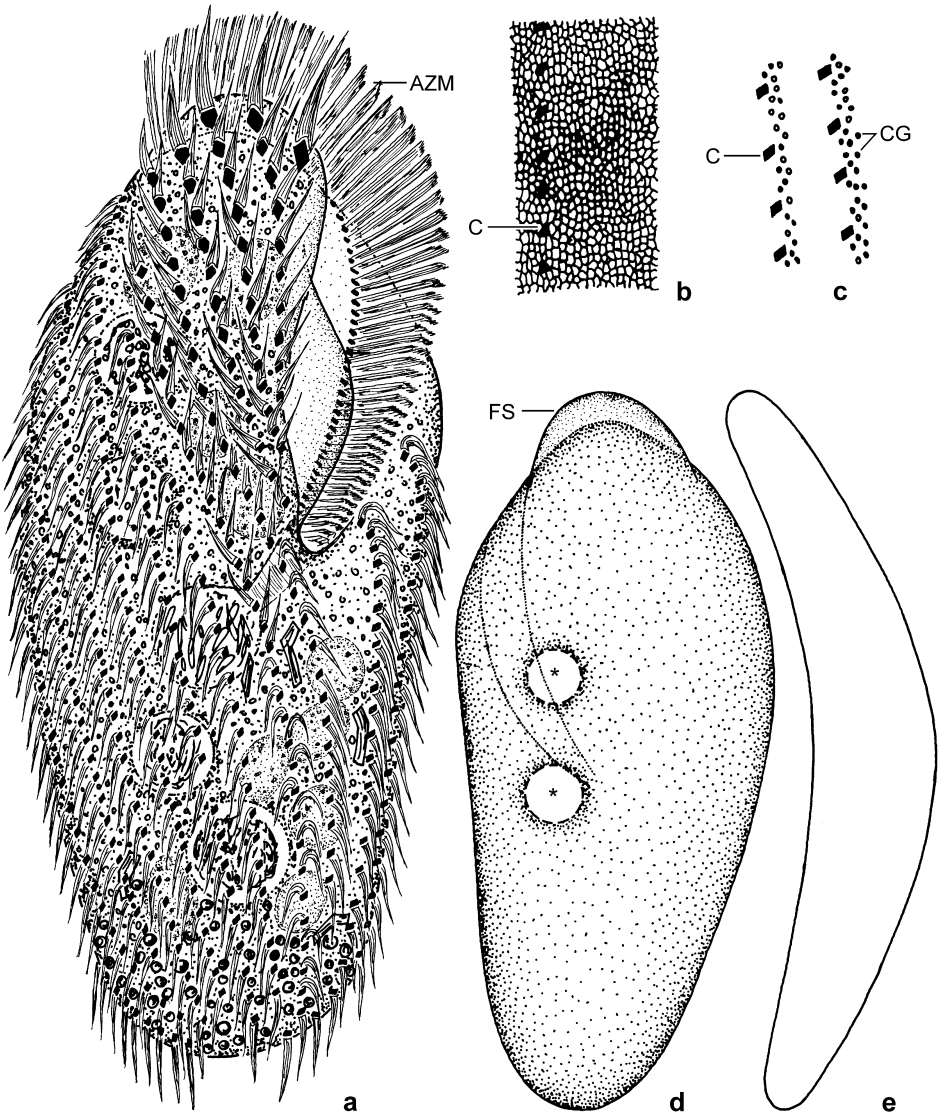


Fig. 109a–e *Pseudokahliella marina* (from Foissner et al. 1982. a, c–e, from life; b, wet silver nitrate impregnation). **a:** Ventral view of a representative specimen, 205 µm. **b:** Silverline system. **c:** Cortical granules along cirral rows. **d:** Dorsal view showing contractile vacuoles (asterisks), 220 µm. **e:** Left lateral view. AZM = adoral zone of membranelles, C = cirrus, CG = cortical granules, FS = frontal scutum. Page 663.

The specimens of the Chinese populations (Hu & Song 2003) are somewhat smaller than those of the type population (Foissner et al. 1982). Further, the dorsal bristles are of rather different length in the type population (2 µm) and Chinese populations (5–6 µm). The Chinese authors found only one undulating membrane and sug-

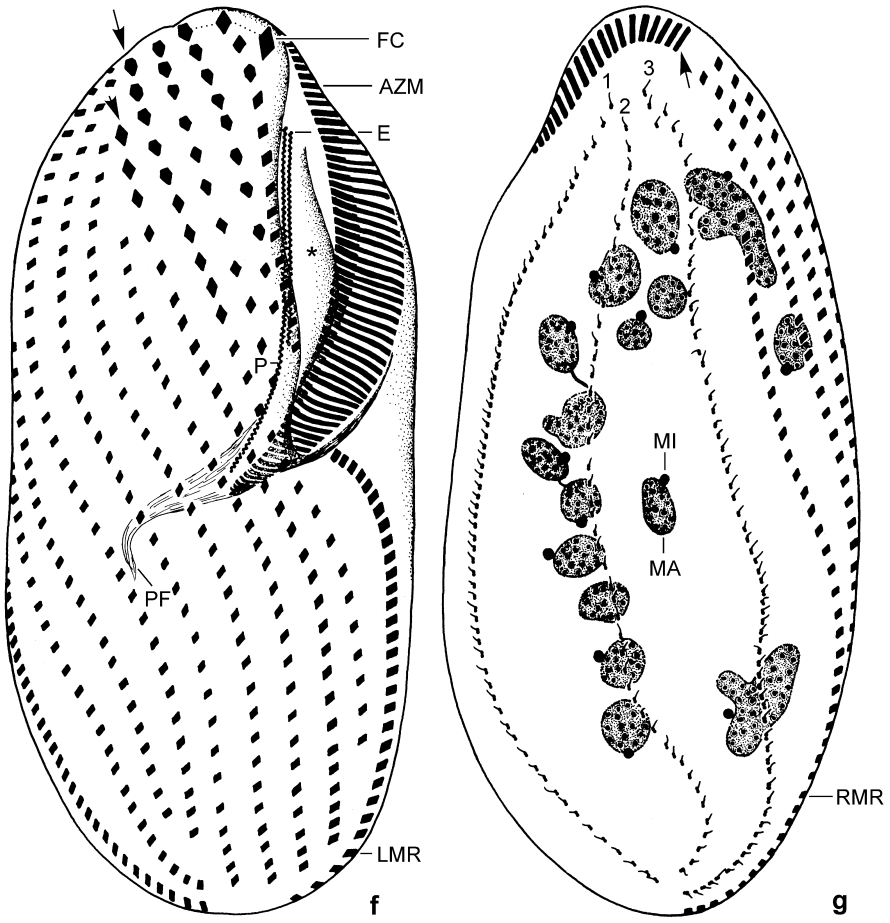


Fig. 109f, g *Pseudokahliella marina* (from Foissner et al. 1982. Protargol impregnation). **f:** Infraciliature of ventral side, 123 µm. Asterisk marks buccal lip. Frontal cirri of anlagen I–III connected by dotted line. Long arrow marks leftmost frontoventral cirral row, which extends onto postoral area; short arrow denotes the rightmost row with somewhat enlarged cirral bases (possible this row is homologous to row VI [anlage I included] of other hypotrichs). Note that this species lacks transverse and caudal cirri (see g). **g:** Infraciliature of dorsal side and nuclear apparatus, 115 µm. Arrow marks distal end of adoral zone. AZM = adoral zone of membranelles, FC = left frontal cirrus, E = endoral, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, P = paroral, PF = pharyngeal fibres, RMR = (outermost) right marginal row, 1–3 = dorsal kineties. Page 663.

gest that the two membranes (paroral and endoral) of the type population (Foissner et al. 1982) are either a "form-variation" or a misinterpretation (Hu & Song 2003, p. 2036). However, it also cannot be excluded that the single row in the Chinese specimens is a malformation or a misobservation/misinterpretation by Hu & Song (2003). Of course it is possible that species exist which have lost one of the two membranes. In this case the loss would be a highly interesting apomorphy for *Pseudokahliella*.

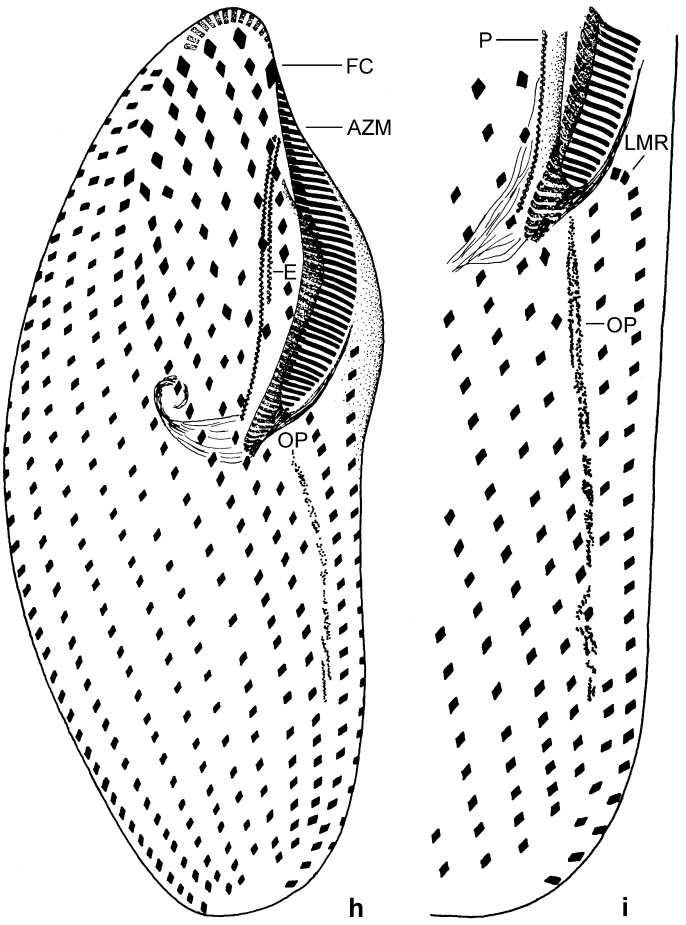


Fig. 109h, i *Pseudokahliella marina* (from Foissner et al. 1982. Protargol impregnation). Infraciliature of ventral side of two very early dividers, h = 160 µm, i = 132 µm. AZM = adoral zone of membranelles, E = endoral, FC = left frontal cirrus, LMR = outermost left marginal row, OP = oral primordium, P = paroral. Page 663.

The second possibility is that *Pseudokahliella* is not a true hypotrich, that is, branched off earlier, namely before the second undulating membrane evolved. The formation of the dorsal kineties via so-called primary primordia and the high relative length of the adoral zone would support this hypothesis; by contrast, the silverline system is fine-meshed as in the Hypotricha, and not (at least partially) wide-meshed as, for example, in the euplotids. Further populations have to be studied to show which of the two descriptions is correct and electron microscopic studies are likely needed to clear up the morphology of the oral apparatus. In addition, meaningful molecular data will be necessary to estimate the phylogenetic position of *P. marina*.

The adoral zone of *Pseudokahliella marina* is very long (about 50% of body length) for a hypotrich which very likely does not belong to the stylonychines, a group of rigid oxytrichids. According to Berger & Foissner (1997) and Berger (1999) a high relative length of the adoral zone is characteristic for this group, but also for the basal group of the spirotrichs, the euplotids. Indeed, due to the increased

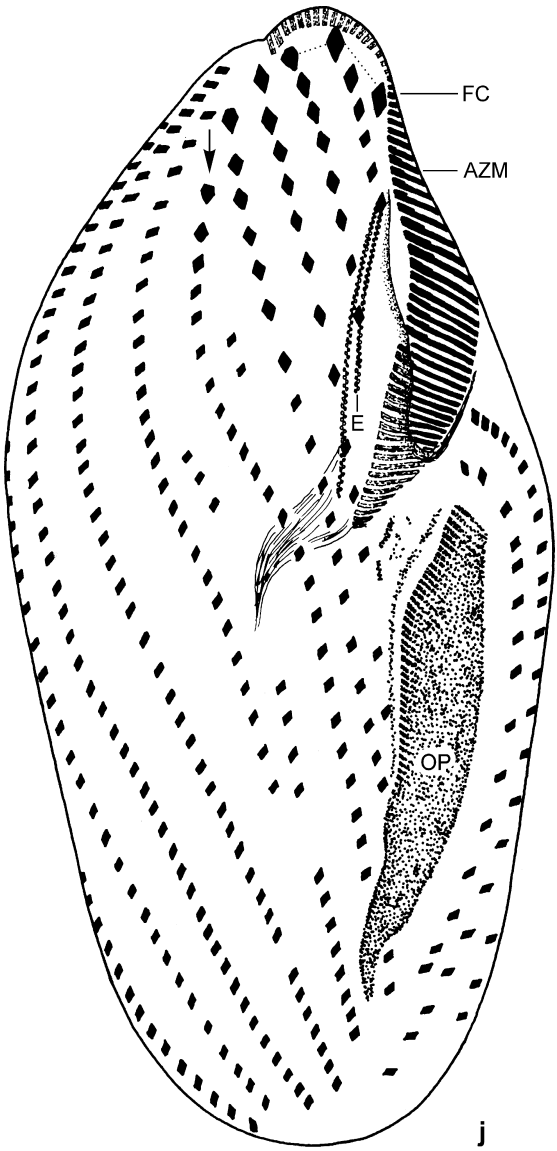


Fig. 109j *Pseudokahliella marina* (from Foissner et al. 1982. Protargol impregnation). Infraciliature of ventral side of an early divider, 130 µm. Arrow marks frontoventral row VI (?; anlage I, that is, left frontal cirrus included). AZM = adoral zone of membranelles, E = endoral, FC = left frontal cirrus, OP = oral primordium. Page 663.

number of cirral rows, *P. marina* (superficially) resembles some curious stylonychines, for example, *Styxophrya quadricornuta* (Foissner, Schlegel & Prescott, 1987) Foissner et al., 2004 and *Gigantothrix herzogi* Foissner, 1999. However, these species have of course a rigid body and a complex dorsal ciliature including a (multiple) fragmentation. Foissner et al. (1982) do not mention the consistency (supple or rigid) of the body. I checked the original notes by Foissner and did not find a hint about the consistence. Hu & Song (2003) wrote “Pellicle thick, but slightly flexible”. I sup-

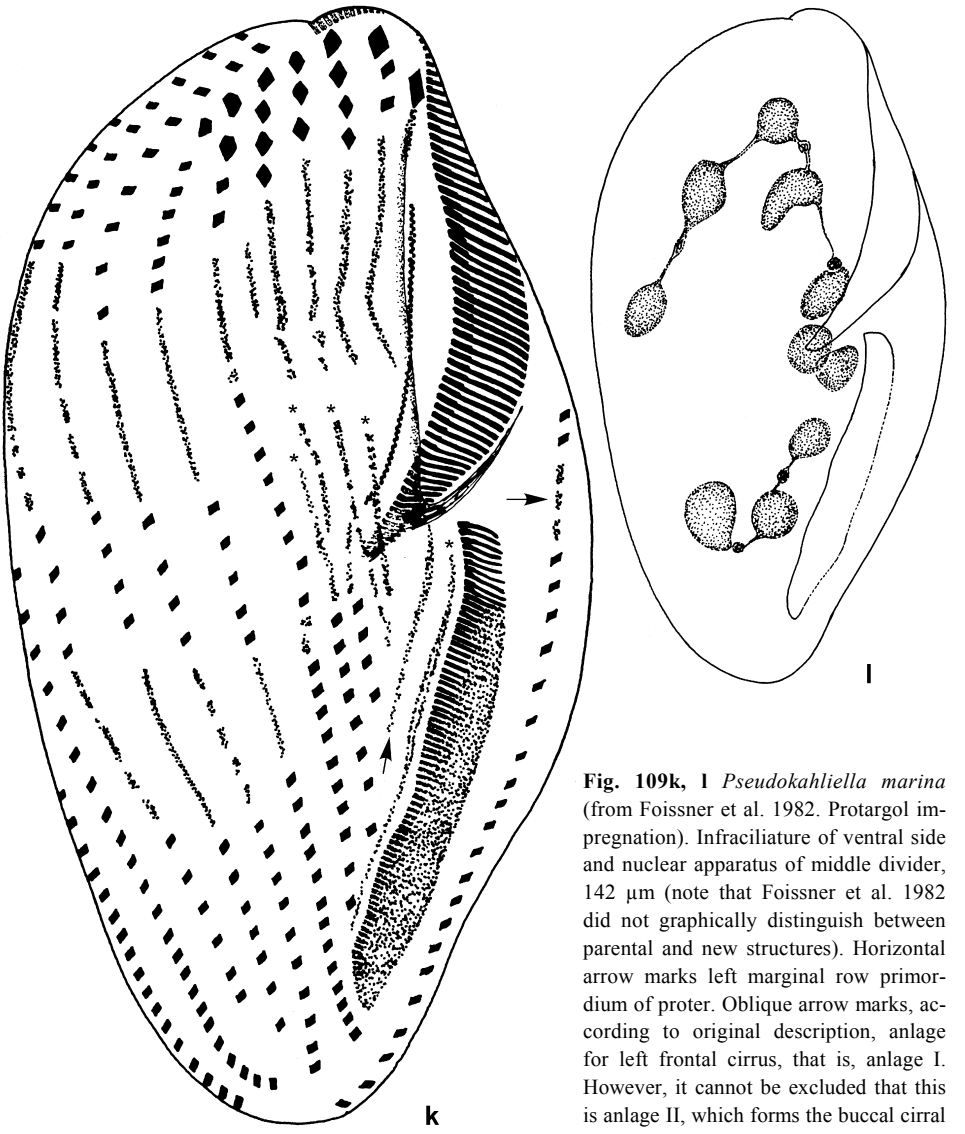


Fig. 109k, l *Pseudokahliella marina* (from Foissner et al. 1982. Protargol impregnation). Infraciliature of ventral side and nuclear apparatus of middle divider, 142 µm (note that Foissner et al. 1982 did not graphically distinguish between parental and new structures). Horizontal arrow marks left marginal row primordium of proter. Oblique arrow marks, according to original description, anlage for left frontal cirrus, that is, anlage I. However, it cannot be excluded that this is anlage II, which forms the buccal cirral row. The asterisks mark, very likely, the anlagen I, III–VI of the opisthe. Possible, all other rows are right marginal rows, which divide individually, that is, each row forms two primordia. Page 663.

pose that *Pseudokahliella marina* is flexible (or maximally semirigid), a feature taken over from the ground pattern of the Hypotricha. However, recent data show that even outside the stylonychines rigid hypotrichs can occur (Foissner & Stoeck 2006). The presence of cortical granules in *P. marina* is a further proof that it does not belong to the stylonychines.

Morphology: Because of the differences discussed in the remarks, the descriptions of the European population and the Chinese populations are not fused. At first the morphology of the type population (Foissner et al. 1982)[1] is described, followed by the characterisation of two Chinese populations studied by Hu & Song (2003).

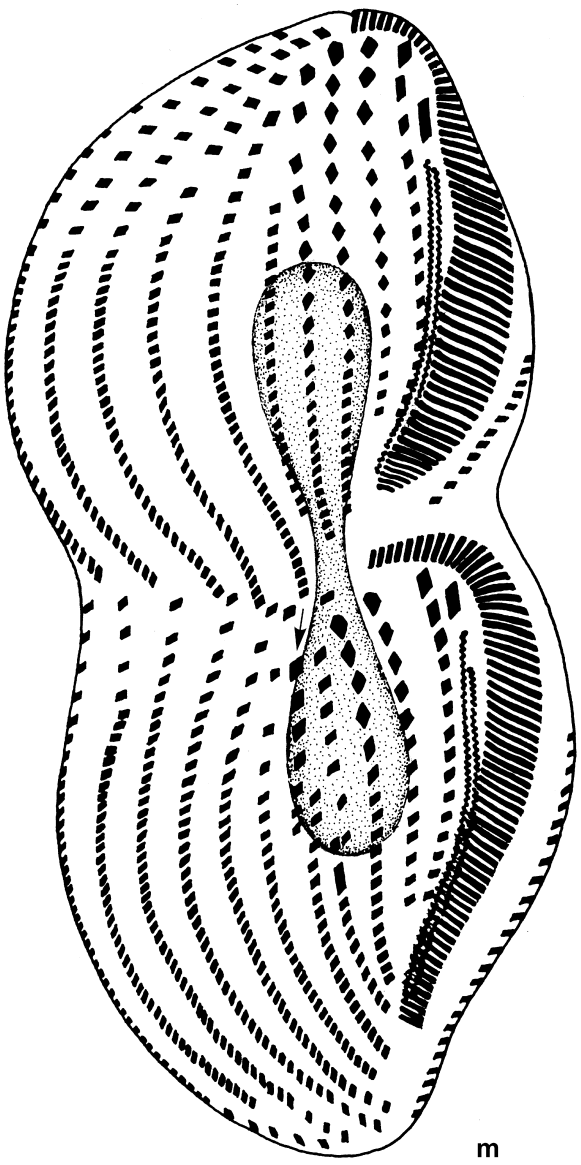
Specimens of type population about 150–230 × 55–75 µm in life, body length to width ratio 2.3:1 in protargol preparations (Table 34). Body outline elliptical, widest at level of greatest size of buccal lip, converging in anteriad and posteriad direction (Fig. 109a, d). Body flattened about 3:1 dorsoventrally, ventral side strongly concave, dorsal side convex (Fig. 109e); not contractile. Macronuclear nodules roughly arranged in inverted C-shaped figure in ventral view (Fig. 109a, g); shape and size of individual nodules rather variable, usually roughly ellipsoidal (Table 34); chromatin bodies very small, numerous. Probably close to each macronuclear nodule a single, small (about 1.5 µm across) micronucleus (Fig. 109g). Two contractile vacuoles about in mid-body and slightly ahead of it, distinctly displaced inwards; possibly connected by a canal (Fig. 109d). Cytopyge subterminal at left cell margin. Cortical granules (protrichocysts?) tiny, colourless, arranged along cirral rows (Fig. 109c). Cytoplasm with many colourless granules about 0.5 µm across, make cells brownish at low magnification. Posterior body portion with accumulation of 1–5 µm-sized, colourless, shining inclusions and some cytoplasmic crystals up to 10 µm long. Movement slow, creeping.

Adoral zone very prominent because occupying 47% of body length and composed of 66 membranelles on average (Fig. 109a, d, f, g, o, Table 34); bases of largest membranelles about 10 µm wide. Membranelles composed of two long rows and one short row of basal bodies, which is a difference to most other hypotrichs where the membranelles are composed of four rows, namely, two long, one short, and one very short. Right proximal portion of zone covered by large, strongly curved buccal lip. Paroral and endoral arranged in parallel, each composed of two narrowly spaced rows of basal bodies. Both membranes commence at 13% and 15% of body length in specimens illustrated (Fig. 109f, h), paroral extends to near proximal end of adoral zone, endoral distinctly shorter[2], namely only about 58% of length of paroral in specimen shown in Fig. 109h. Note that the Chinese populations have only one undulating membrane (perhaps a misobservation; see remarks).

Cirral pattern and number of cirri of usual variability for hypotrichs with such a high number of cirri (Fig. 109a, f, h, Table 34). Three frontal cirri and several other cirri on frontal area rather strong and 15–20 µm long. All other cirri about 10 µm long. Whole ventral surface covered by cirri arranged in up to 15 more or less oblique and/or sigmoidal rows; since the number of rows is variable, a unambiguous designation of the individual rows is not possible. Left frontal cirrus distinctly enlarged, slightly behind level of remaining two frontal cirri. 2–4 shortened frontoventral rows ending ahead of proximal portion of adoral zone. Next rows extend onto

[1] Note that in the original description left and right are sometimes confused.

[2] Hu & Song (2003, p. 2036) incorrectly wrote that the undulating membranes of the type population are of equal length.



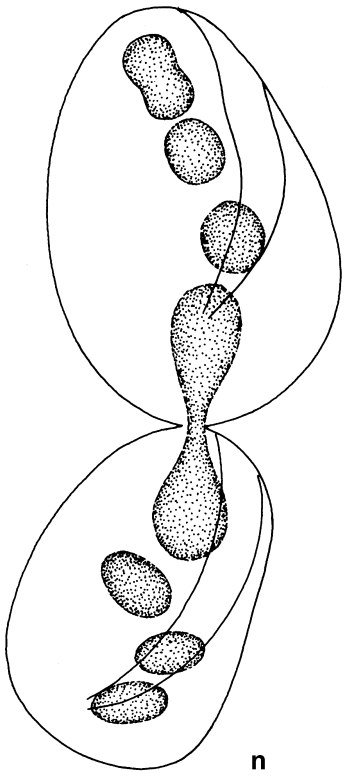


Fig. 109m, n *Pseudokahliella marina* (from Foissner et al. 1982. Protargol impregnation). **m:** Infraciliature of a very late divider, 145 µm. Arrow marks the frontoventral row VI of the opisthe (note that Foissner et al. 1982 did not graphically distinguish between parental and new structures). **n:** Nuclear apparatus of a very late divider, 140 µm. Page 663.

rear body portion. Anteriormost cirri of 5–6 leftmost frontoventral rows (left frontal cirrus included) more or less distinctly enlarged. Next rows anteriorly shortened, adjoin in acute angle to remaining rows producing a distinct suture. Outermost rows on right margin extend onto dorsolateral surface anteriorly. It is difficult to decide – even with ontogenetic data – what is a marginal row and what is a frontoventral row (see below). One or two left marginal rows, commence left of proximal portion of

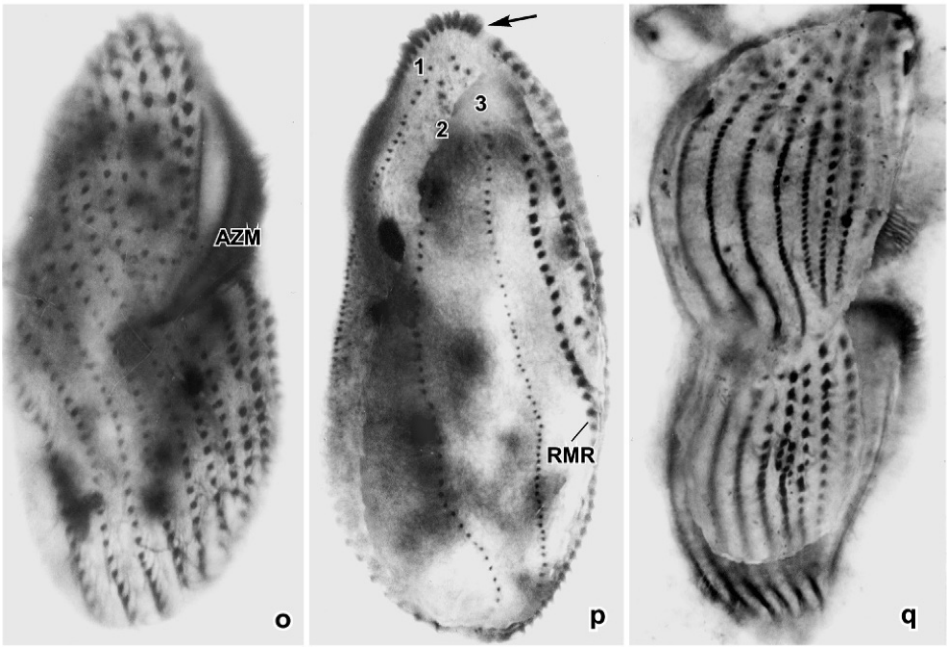


Fig. 109o–q *Pseudokahliella marina* (from Foissner et al. 1982. Protargol impregnation). **o, p**: Infraciliature of ventral and dorsal side. Arrow in (p) marks distal end of adoral zone of membranelles. **q:** Infraciliature of ventral side of a late divider. AZM = adoral zone of membranelles, RMR = outermost right marginal row, 1–3 = dorsal kineties. Page 663.

adoral zone and extend roughly J-shaped to near rear body end; cirri rather strong and narrowly spaced (Fig. 109f). Transverse cirri lacking.

Dorsal bristles about 2 µm long and stiff, invariably arranged in three kineties of body length. Basal body pairs within kineties very narrowly spaced; anterior basal body of each pair ciliated. Caudal cirri lacking (Fig. 109a, g, p, Table 34).

Silverline system of whole cell composed, as is usual for hypotrichs, of fine meshes; meshes 0.5–0.7 µm in size, usually polygonal (Fig. 109b).

Morphology of two populations from the Yellow Sea near Qingdao, China (Fig. 110a–j, Table 34): Body size about 120–175 × 50–75 µm. Body outline rather constant, that is, broad elliptical with both ends rounded; left margin nearly straight to slightly concave, right margin always convex (Fig. 110a–c). Body dorsoventrally flattened 3:1 (Fig. 110d). Macronucleus more or less as in type population, that is, 9–20 nodules arranged inverted C-shaped in ventral view; individual nodules ovoid to ellipsoidal, about 12 × 9 µm in protargol preparations. 4–8 micronuclei, each about only 1.5 µm across, often very near to macronuclear nodules (Fig. 110a, i). Contractile vacuole not observed in life. Pellicle thick, but slightly flexible. Cortical granules (extrusomes), although colourless, conspicuous because about 1 µm across; arranged in longitudinal rows; spindle-shaped and about 5–7 µm long when ejected

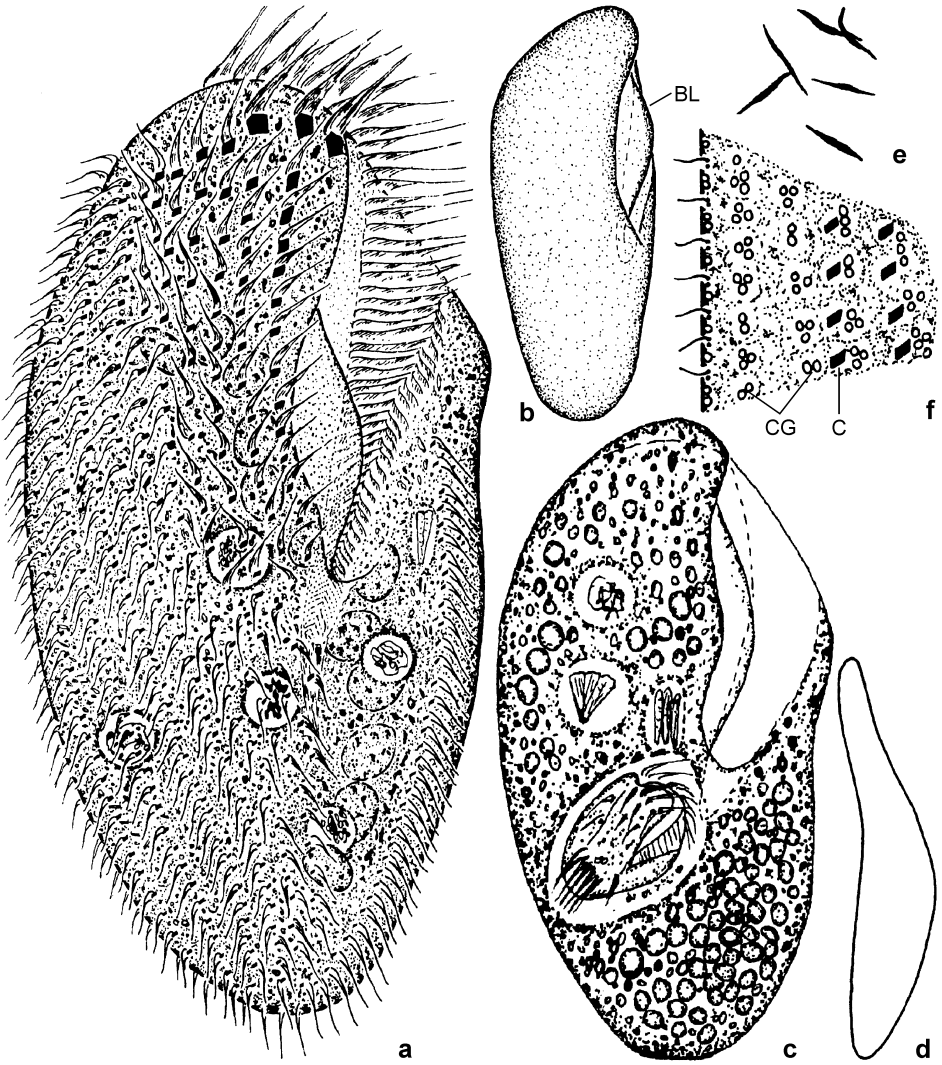


Fig. 110a–f *Pseudokahliella marina* (from Hu & Song 2003. From life). **a:** Ventral view, 175 µm. **b:** Ventral view showing buccal lip. **c:** Cell inclusions like food vacuoles (inter alia, with a euplotid) and granular inclusions. **d:** Left lateral view, 200 µm. **e:** Ejected cortical granules, about 7 µm long. **f:** Cell surface showing arrangement of cortical granules. BL = buccal lip, C = cirri, CG = cortical granules. Page 663.

(Fig. 110e, f). Cytoplasm usually dark greyish, especially in posterior body portion with many refractive and granular inclusions, make cells opaque at low magnification; several large food vacuoles (Fig. 110a, c). Movement without peculiarities, that is, moderately rapid, usually creeping or sometimes swimming spirally around main body axis.

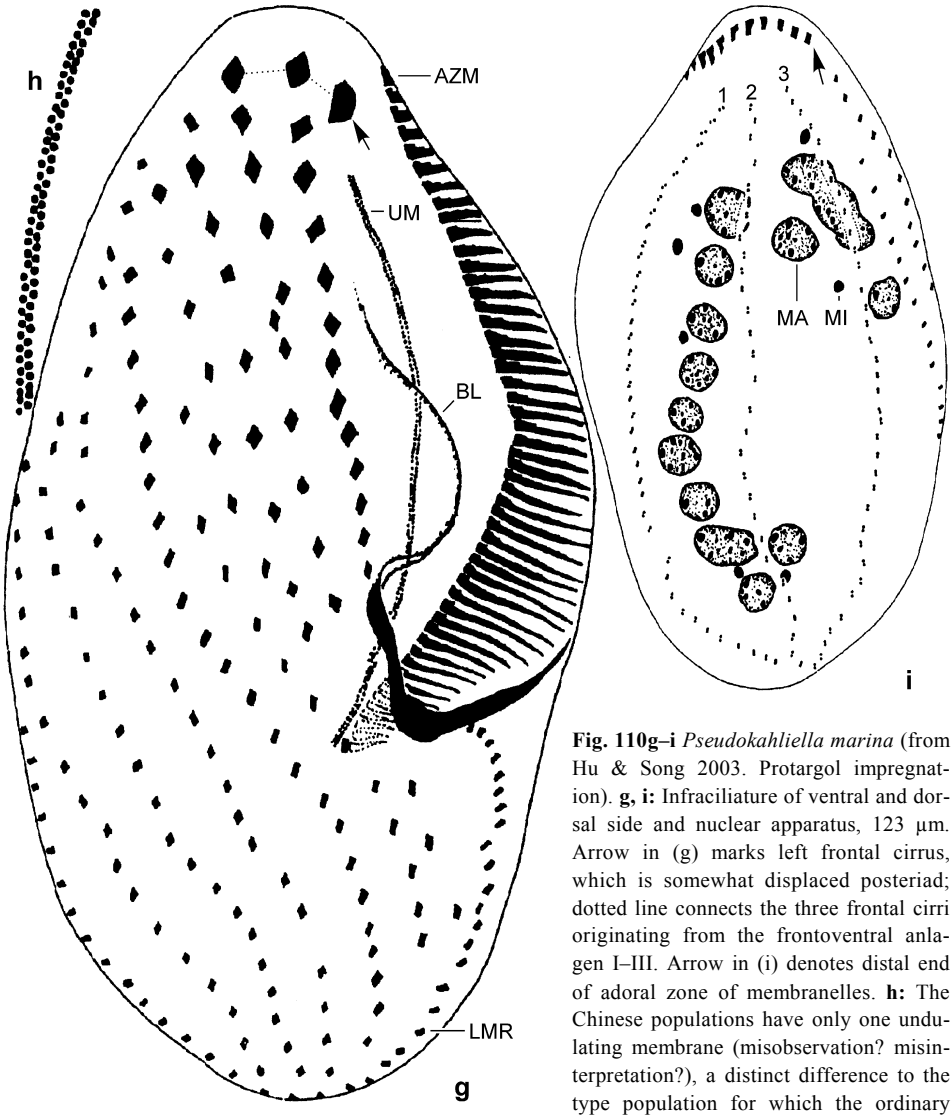


Fig. 110g–i *Pseudokahliella marina* (from Hu & Song 2003. Protargol impregnation). **g, i:** Infraciliature of ventral and dorsal side and nuclear apparatus, 123 µm. Arrow in (g) marks left frontal cirrus, which is somewhat displaced posteriad; dotted line connects the three frontal cirri originating from the frontoventral anlagen I–III. Arrow in (i) denotes distal end of adoral zone of membranelles. **h:** The Chinese populations have only one undulating membrane (misobservation? misinterpretation?), a distinct difference to the type population for which the ordinary number of two membranes is described. AZM= adoral zone of membranelles, BL = buccal lip, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, UM = undulating membrane, 1–3 = dorsal kineties. Page 663.

Adoral zone very conspicuous because 40–50% of body length and composed of 58, respectively, 50 membranelles on average which is slightly less (66) than in type population; cilia of membranelles up to 20 µm long (Fig. 110a, c, g, Table 34). Buccal field occupies about one third of body width; buccal lip ("roof-like structure" in paper by Hu & Song 2003) covers rear portion of adoral zone. Only one(!) undulating membrane, made of two rows narrowly spaced basal bodies (Fig. 110g, h); note

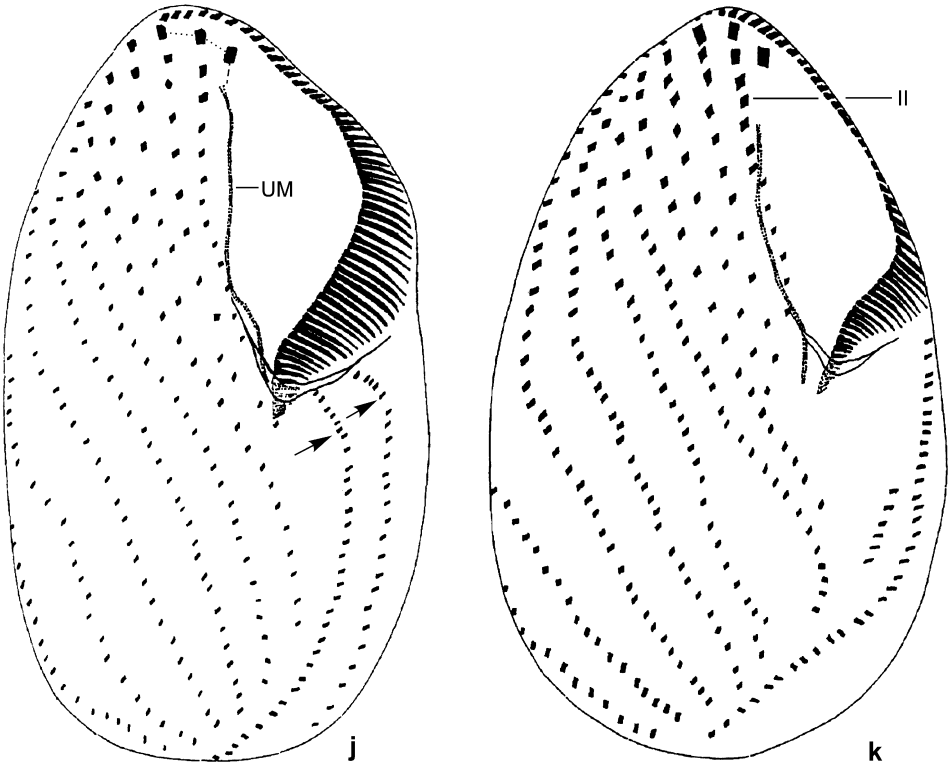


Fig. 110j, k *Pseudokahliella marina* (from Hu & Song 2003. Protargol impregnation). Infraciliature of ventral side of a specimen with two complete left marginal rows (j, arrows; size not indicated) and a specimen (k; 164 µm) with one complete row and one very short fragment. Broken line in (j) indicates that the left frontal cirrus originates from the same anlage as the undulating membrane; dotted line connects the three frontal cirri. Note that for the Chinese populations only one undulating membrane is described. UM = undulating membrane, II = frontoventral row II (= buccal cirral row). Page 663.

that the type population has the plesiomorphic number of two membranes (see remarks). Pharyngeal fibres about 25 µm long after protargol impregnation.

Frontal cirri strong, 15–18 µm long, remaining cirri comparatively fine and only 10–12 µm long. Cirral pattern as shown in Fig. 110a, g, j, k, that is, basically as in type population. Invariably three distinctly enlarged frontal cirri. Usually 7–10 frontoventral rows (left frontal cirrus likely not included) plus each one left and right marginal row. Anterior portion of rightmost rows extending onto dorsolateral surface. Rarely (in five specimens of more than 50) two left marginal rows or one row plus one fragment (Fig. 110j, k). Transverse cirri lacking.

Dorsal cilia about 5–6 µm long[1], narrowly spaced, invariably arranged in three kineties of body length. Caudal cirri lacking (Fig. 110i).

[1] According to Fig. 110f the dorsal bristles are only about 3 µm long because they are about three times as long as the cortical granules, which are about 1 µm across. Of course this estimation resumes that the

Cell division: Morphogenesis of cell division was studied by Foissner et al. (1982; Fig. 109h–n, q) and Hu & Song (2003; Fig. 110l–q; some stages not shown in present book because identical with that of type population).

Morphogenesis commences with the formation of a slender, epiapokinetal oral primordium between the (inner) left marginal row and the leftmost frontoventral rows which extend posteriorly beyond the buccal vertex (Fig. 109h, i; Song 2004, p. 748; Foissner 1996, p. 107, designated the stomatogenic mode as "parakinetal?"). Later, the oral primordium increases and extends from near the proximal end of the parental adoral zone to near the rear cell end (Fig. 109j). On the right side of the oral primordium, the anlage for the undulating membranes (= anlage I) and for the two next anlagen (II, III; Foissner et al. 1982 designated them erroneously as right ventral rows) are formed. Fig. 109k, l show a late divider with well-developed primordia for the proter and the opisthe. It is rather difficult to decide which anlagen are frontoventral rows and which are marginal rows. No (distinct) reorganisation occurs in the parental adoral zone, which is retained for the proter. The new undulating membranes of the proter originate from the modified parental undulating membranes (Fig. 109k, m).

Foissner et al. (1982) did not study the formation of the dorsal kineties. By contrast, Hu & Song (2003) described the dorsal morphogenesis (Fig. 110o, q), but could not observe the very first stage. Thus, it is not known whether per parental kinety only one anlage (a so-called primary primordium, which later divides) is formed, or two more or less distinctly separated anlagen. Cell division clearly shows that P. marina lacks caudal cirri.

The nuclear apparatus divides in the ordinary manner, that is, the macronuclear nodules fuse to a single mass and later divide (Fig. 109l–n). Hu & Song (2003, p. 2042) mentioned that not stage with a fused macronucleus was illustrated in the original description. However, this statement is incorrect because Fig. 109m clearly shows that all macronuclear nodules fuse to a single mass.

Hu & Song (2003) discussed some details of cell division, inter alia, that the frontoventral and marginal rows in both filial products originate from anlagen within the parental rows, and that no parental rows are retained after division. It is a common feature in hypotrichs that a certain anlage originates within the parental structure (see Table 4 in Berger et al. 1985 and Table 4 in Berger 1999). Of course, deviations occur, for example, opisthe's anlagen I–III, which usually originate from the oral primordium (for overviews, see Berger et al. 1985, Berger & Foissner 1997, Berger 1999). A further feature discussed by Hu & Song (2003) is the fact that in the Chinese populations only one undulating membrane is formed. This observation is difficult to interpret, inasmuch as the type population obviously has an endoral and a paroral (Foissner et al. 1982; see remarks).

Occurrence and ecology: Marine (Foissner et al. 1982, Patterson et al. 1987, Hu & Song 2003). Type locality of *Pseudokahliella marina* is the coast of the Mediterranean Sea about 2 km north of the village of Banyuls-sur-Mer, France, where

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full length of the bristles is shown and the structures are drawn to scale.

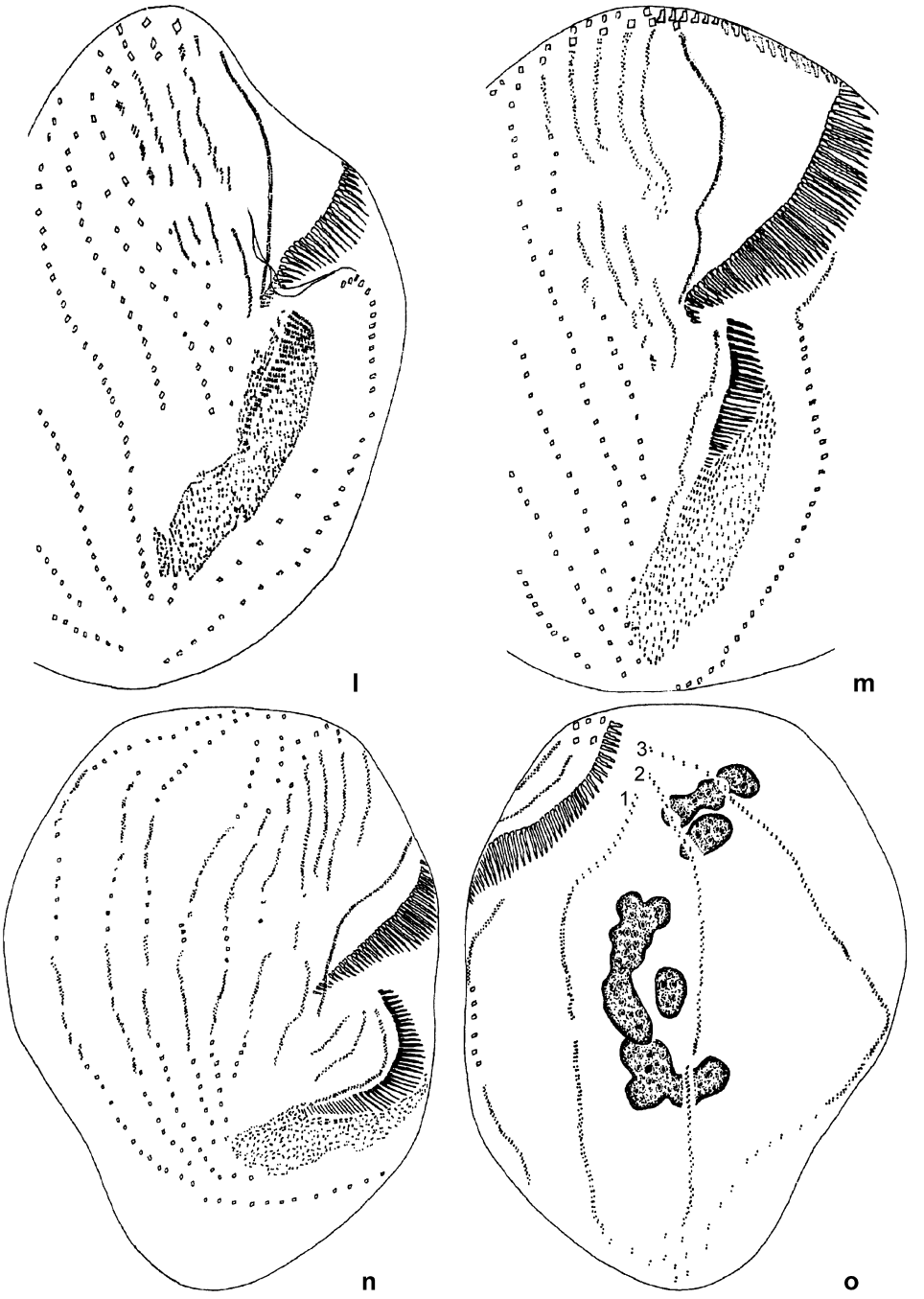

Fig. 110l–o *Pseudokahliella marina* (from Hu & Song 2003. Protargol impregnation). Parental structures white, new black. **l, m:** Infraciliature of ventral side of early dividers, l =159 µm, m = 90 µm. **n, o:** Infraciliature of ventral and dorsal side and nuclear apparatus of a middle divider, 95 µm. 1–3 = dividing dorsal kineties. Page 663.

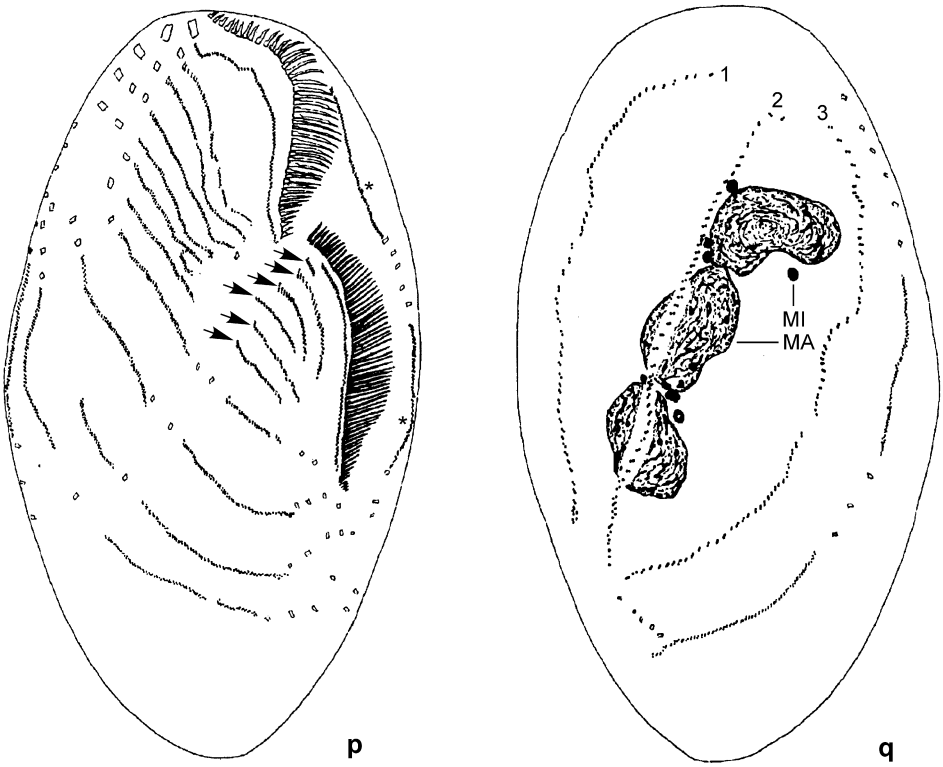

Fig. 110p, q *Pseudokahliella marina* (from Hu & Song 2003. Protargol impregnation). Infraciliature of ventral and dorsal side and nuclear apparatus of a middle to late divider, 98 µm. Arrows in (p) mark six frontoventral cirri anlagen (including undulating membrane anlage), which are probably homologous to the ordinary six anlagen (I–VI) of the Hypotricha ground pattern. The remaining rows originate by intrakinetal proliferation and are therefore very likely "right marginal rows". MA = macronucleus, MI = micronucleus, 1–3 = dorsal kineties. Page 663.

Foissner et al. (1982) discovered it in a several-days old infusion with fouling leaves and algae from a flood-pond. Hu & Song (2003) found two populations in 1996 and 2000 in mollusc-culturing waters along the coast of Qingdao (36°08´N 120°43´E), China. Record not substantiated by morphological data: coastal area of the Sea of Cantabria (Spain), Bay of Biscay, Atlantic Ocean (Fernandez-Leborans & Novillo 1993, p. 216).

Pseudokahliella marina feeds on algae and ciliates like *Vorticella* sp. and *Cyclidium* sp. (Foissner et al. 1982), but also on bacteria, diatoms, and euplotids (Fig. 110a, c; Hu & Song 2003).

Stenotricha Jankowski, 1978

1978 ***Stenotricha* gen. n.** – Jankowski[1], Tezisy Dokl. zool. Inst. Akad. Nauk. SSSR, year 1978: 40 (original description). Type species (by original designation): *Strongylidium arenicolus* Dragesco, 1953.
1979 ***Stenotricha* Jk., 1978** – Jankowski, Trudy zool. Inst., Leningr., 86: 65 (generic catalogue of hypotrichs).
2001 ***Stenotricha* Jankowski, 1978** – Aescht, Denisia, 1: 153 (catalogue of generic names of ciliates; see nomenclature).
2001 ***Stenotricha* Jankowski, 1978** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 80 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).
2007 ***Stenotricha* Jankowski, 1978** – Jankowski, Phylum Ciliophora, p. 460 (generic revision of ciliates; see nomenclature).
2008 ***Stenotricha* Jankowski, 1978** – Lynn, Ciliated protozoa, p. 362 (revision of ciliate families).

Nomenclature: No derivation of the genus-group name is given in the original description. *Stenotricha* is a composite of the Greek adjective *stenós* (narrow, small) and the Greek noun *he thrix*, *trichós* (genitive; hair; likely cirrus/cirri in present case). I do not know to which part/feature of the infraciliature the name refers. Feminine gender (Aescht 2001, p. 301). According to Aescht (2001), type fixation is by monotypy. However, Jankowski (1978) wrote "*Stenotricha* n. gen. for *Strongylidium arenicolus* Dragesco" which is actually a fixation by original designation. Jankowski (1978) provided a very short characterisation[2], thus, *Stenotricha* is very likely validly published (ICZN 1964, Article 13(a)).

Characterisation (A = supposed apomorphy): Hypotrich of unknown systematic position with cephalised (A?) body. Adoral zone of membranelles prominent, formed like a question mark, that is, distal end far extending posteriorly. Three prominent frontal cirri. Buccal cirrus lacking? (A?). Short row of parabuccal(?) cirri behind/close to right frontal cirrus and short cirral row commencing right of buccal vertex (postoral ventral cirri?). Transverse cirri present, prominent. One left and one right marginal row. Marine psammon.

Remarks: See single species.

Species included in *Stenotricha* (basionym is given): (1) *Strongylidium arenciolus* Dragesco, 1953 (type species).

Single species

Stenotricha arenicola (Dragesco, 1953) Jankowski, 1978
(Fig. 111a–e)

1953 ***Strongyllidium arenicola* nov. sp.** – Dragesco, Vie Milieu, 4: 629 (nomen nudum and incorrect subsequent spelling of *Strongylidium*; see nomenclature).

[1] According to the Zoological Record (1979, vol. 116, p. 144) the name of the author is A.V. Yankovskij. Here I use the ordinary spelling A.W. Jankowski, which is used, for example, in Jankowski (1979, p. 85; 2007).

[2] I could not translate the characterisation in detail, but obviously it refers to the cephalisation of *S. arenicola*.

1953 ***Strongylidium arenicolus* nov. sp.**[1] – Dragesco, Vie Milieu, 4: 637, Fig. In (Fig. 111a; original description; no type material available according to Aescht 2001, p. 195).

1960 ***Strongylidium arenicolus* Dragesco** – Dragesco, Trav. Stn biol. Roscoff, , 122: 308, Fig. 164a–d (Fig. 111b–e; detailed description).

1972 ***Strongylidium arenicolus* Dragesco, 1953** – Borror, J. Protozool., 19: 18, Fig. 63 (schematic redrawing of Fig. 111b; revision of hypotrichs).

1978 ***Strongylidium arenicolus* Dragesco** – Jankowski, Tezisy Dokl. zool. Inst. Akad. Nauk. SSSR, year 1978: 40 (combination with *Stenotricha*; see nomenclature).

1979 ***Strongylidium arenicolus* Dragesco, 1953** – Jankowski, Trudy zool. Inst., Leningr., 86: 65 (generic catalogue of hypotrichs).

1982 ***Strongylidium arenicolus* Dragesco, 1954** – Hemberger, Dissertation, p. 278 (revision of hypotrichs).

1992 ***Strongylidium arenicola* Dragesco, 1953** – Carey, Marine interstitial ciliates, p. 175, Fig. 691 (redrawing of Fig. 111a, b; guide to psammophilous ciliates).

2001 ***Stenotricha arenicola* nom. corr.** – Aescht, Denisia, 1: 153 (catalogue of generic names of ciliates; mandatory change of gender ending, that is, nomen corrigendum).

2001 ***Stenotricha arenicola* (Dragesco, 1954) Jankowski, 1978** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 82 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: No derivation of the name is given in the original description. The species-group name *arenicol·us*, *-a*, *-um* (Latin adjective [m; f; n]; living in sand, sand-inhabiting) obviously alludes to the habitat ([marine] sand) where the species was discovered. The name in Dragesco (1953a)[2] is neither accompanied by a description nor by a hint to such a description and therefore it is a nomen nudum (ICZN 1999, Article 13). Jankowski (1978) did not formally transfer *Strongylidium arenicolus* to *Stenotricha*. However, since he fixed it as type species of *Stenotricha* he automatically is the combining author (Berger 2001). *Strongylidium* is neuter, *Stenotricha* is feminine (Aescht 2001). Thus, Aescht (2001) correctly adjusted the species-group name. When the original classification is retained then the correct name is *Strongylidium arenicolum* nom. corr. Patterson et al. (1989, p. 210) incorrectly assumed that Dragesco (1960) is the author of the species.

Remarks: This is a little known, but conspicuous marine hypotrich. Dragesco (1953) classified it in *Strongylidium* Sterki, 1878, a difficult, inhomogenous genus, inter alia, because its type species is not known in detail (Kahl 1932, Borror 1972, Paiva & Silva-Neto 2007). Borror (1972) and Hemberger (1982) obviously did not agree with the original classification in *Strongylidium* and therefore listed it as valid species of questionable systematic position, however, without removing it formally from *Strongylidium*. The cephalised, usually non-twisted body, the cirral pattern (lack of long, spiralling frontoventral rows), and very likely also the marine habitat prevent a classification in *Strongylidium* or another genus. Thus, I agree with Jan-

[1] Dragesco (1953) provided the following characterisation: Plat, thygmotactique, transparent. Grande frange adorale, trois puissants cirres latéraux. Macronuclei (au nombre de 4) symétriquement disposés de part et d'autre du micronucleus. Longueur: 170 µm.

[2] The papers Dragesco (1953, 1953a) are either dated with 1953 (e.g., Borror 1972) or 1954 (e.g., Dragesco 1960, Aescht 2001). I have a copy of the cover of issue 4 of the journal Vie et Milieu in which both papers appeared, and this issue is dated with 1953.

kowski (1978, 1979) to classify it in an own, so far monotypic genus (*Stenotricha*), a proposal also accepted by Paiva & Silva (2007, p. 53) in their brief review on *Strongylidium*.

I found no higher-level classification in the original description or later papers. Just Jankowski (2007) classified it in the Amphisiellidae Jankowski, 1979, whereas Lynn (2008) mentioned it as incertae sedis in the Stichotrichia (= Hypotricha of present monograph). At present, it is actually not possibly to make a serious comment about the phylogenetic position because the dorsal kinety pattern and details of the ventral ciliature are not known. Thus, I "classify" *Stenotricha arenicola* as incertae sedis in the Hypotricha. According to the general habitus (e.g., cephalised anterior end, strong transverse cirri) it could be a discocephalid. As usual in such cases, much more detailed data are needed for a reliable classification.

The short parabuccal row, the postoral ventral cirri, and the lack of long frontoventral rows are reminiscent of *Apourosomoida*, a genus comprising five species from highly saline habitats (p. 684). However, the cephalised anterior end, the strong transverse cirri, and very likely also the habitat (marine sand vs. usually highly saline habitats like, for example, salt lakes) show that synonymy can be excluded.

Morphology: The original description is very short and incomplete (Dragesco 1953). Thus, the following review is based on the much more detailed characterisation by Dragesco (1960). Most values (e.g., number of cirri) are from Fig. 111b, that is, these data must not be overinterpreted. Body length 170 µm, specimen illustrated about 156 × 19 µm, that is, length:width ratio about 8.2:1 (Fig. 111b). Body outline band-shaped, that is, margins in parallel; anterior portion more or less distinctly cephalised (disc-shaped), rear portion suddenly narrowed and narrowly rounded. Body flat, transparent, thigmotactic, and sometimes twisted (Fig. 111c). Flexibility of cell not described. Nuclear apparatus obviously highly distinct because composed of two pairs of macronuclear nodules with single micronucleus in between (Fig. 111d); each macronuclear pair consists of a distal sphere and a proximal ellipsoid. Contractile vacuole, as is usual, near left cell margin, but distinctly displaced posteriad; in specimen illustrated at 62% of body length (Fig. 111b). Cytoplasm transparent and packed with food vacuoles and some ingested grains of sand. Cell almost entirely covered with elliptical scales that disappear slowly in morbid specimens (Fig. 111e); size of scales not indicated. The scales are a highly interesting feature which has to be carefully checked in a redescription because it cannot be excluded that these are subcortical structures (mitochondria?) also present in some other hypotrichs, for example, *Urosoma* (Berger & Foissner 1989a, Berger 1999) and *Uroleptopsis* (Berger 2004, 2006a).

Adoral zone formed like a question mark, that is, distal end extending to near neck on right body margin, proximal end at about 23% of body length in specimen illustrated, composed of about 37 membranelles which are most prominent on the curved anterior portion of the head region (Fig. 111b; however, note that this value must not overinterpreted because it is from a live illustration). Undulating membrane

(paroral) rather prominent, extends more or less straight from near left frontal cirrus to buccal vertex and forming right margin of long-triangular buccal field/cavity.

Cirral pattern obviously easily recognisable in life because specimens rather large. Three very prominent frontal cirri on "head" region forming triangular pattern. Obviously no buccal cirrus. Five parabuccal(?) cirri form short row commencing right of right frontal cirrus (note that the parabuccal cirri are usually more or less exactly behind the right frontal cirrus). Longitudinal row of postoral(?) ventral cirri commencing right of buccal vertex, that is, at 23% of body length in specimen illustrated, terminating at about 34% and composed of seven cirri. Three strong and 25 µm long transverse cirri on narrowed rear end and therefore distinctly protruding beyond cell end; Dragesco (1960) designated them as caudal cirri, which is likely incorrect because they are, according to the illustration, inserted on the ventral side (Fig. 111b). Right marginal row composed of 39 cirri, commences at neck, runs exactly parallel to cell margin, terminates – like left marginal row – at base of short tail (Fig. 111b). Left marginal row composed of 33 cirri, begins left of buccal vertex.

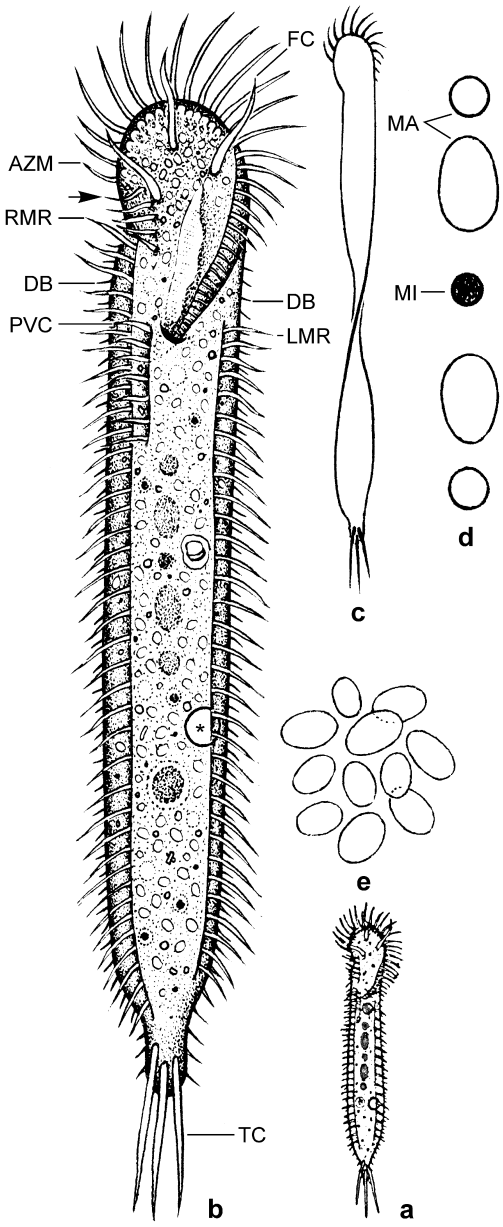

Fig. 111a–e *Stenotricha arenicola* (a, from Dragesco 1953; b–e, from Dragesco 1960. From life). **a, b:** Ventral views, b = 156 µm. Arrow marks short (parabuccal?) row close to (behind?) right frontal cirrus. Asterisk marks contractile vacuole. **c:** Twisted specimen showing strong dorsoventral flattening. **d:** Nuclear apparatus composed of two pairs of macronuclear nodules with single micronucleus in between. **e:** Elliptical scales covering the cell (see text). AZM = distal end of adoral zone of membranelles, DB = dorsal bristles (see text), FC = left frontal cirrus, LMR = left marginal row, MA = macronuclear nodules forming anterior pair, MI = micronucleus, PVC = postoral ventral cirri (see text), RMR = right marginal row, TC = transverse cirri. Page 680.

Fig. 111b shows bristles on each margin, likely dorsal cilia, although termed cirri by Dragesco (1960). Length of dorsal bristles (at least 2 µm according to Fig. 111b), number and arrangement of kineties, and presence/absence of caudal cirri neither mentioned nor illustrated.

Occurrence and ecology: *Stenotricha arenicola* is likely confined to fine sediments of marine habitats (for review, see Patterson et al. 1989, p. 210). Type locality is the fine sand at the beach of Banyuls-sur-Mer (France), Mediterranean Sea (Dragesco 1953). Records not substantiated by morphological data: mainly from June to November with a biomass of up to 156 mg C m^{-3} in the San Marcos Beach (Santoña; Spain), bordering the Sea of Cantabria, Bay of Biscay, Atlantic Ocean (Fernandez-Leborans & Fernandez-Fernandez 1999, p. 633; as *Strongylidium arenicola*); Brazomar Beach and other beaches in the Castro Urdiales area (Spain), Sea of Cantabria, Bay of Biscay, Atlantic Ocean (Fernandez-Leborans & Novillo 1994, p. 203; 1994a, p. 27; Fernandez-Leborans et al. 1999, p. 742; Fernandez-Leborans 2000, p. 417).

Stenotricha arenicola feeds on flagellates (Dragesco 1960, Fenchel 1968, p. 117), and tolerates 1 mg l^{-1} lead (Fernandez-Leborans 1994, p. 203).

Supplement to *Apourosomoida*

Apourosomoida Foissner, Agatha & Berger, 2002

2002 ***Apourosomoida* nov. gen.** – Foissner, Agatha & Berger, Denisia, 5: 759 (original description). Type species (by original designation): *Apourosomoida halophila* Foissner, Agatha & Berger, 2002.

2007 ***Apourosomoida* Foissner, Agatha et Berger, 2002** – Jankowski, Phylum Ciliophora, p. 468 (generic revision of ciliates; see nomenclature).

2008 ***Apourosomoida* Foissner, Agatha & Berger, 2002** – Berger, Monographiae biol., 88: 514 (detailed review).

2008 ***Apourosomoida* Foissner, Agatha & Berger, 2002** – Lynn, Ciliated protozoa, p. 360 (revision of ciliate families).

Nomenclature: See Berger (2008, p. 514).

Characterisation (A = supposed apomorphy): Hypotrich of unknown systematic position. Adoral zone of membranelles with gap at left anterior corner of body. Undulating membranes roughly in *Gonostomum* pattern. Three frontal cirri. Buccal cirrus present. Usually four frontoventral cirri in L-shaped pattern. Postoral cirral row present, formed only by anlage IV (A). Pretransverse ventral cirri lost and number of transverse cirri strongly reduced. One left and one right marginal row. Two dorsal kineties. Caudal cirri present. Frontal-ventral-transverse cirri anlage V lost (A?). Anlagen IV and VI are primary primordia. Dorsal kinety formation in *Apourosomoida* pattern[1] (A). Highly saline habitat.

[1] For detailed description of this pattern, see cell division of *A. halophila* in Foissner et al. (2002a, p. 761) or Berger (2008, p. 516) (Note: a dorsomarginal kinety and an oxytrichid kinety fragmentation are lacking!).

Additional characters: Body slender, flexible; two or four macronuclear nodules; no contractile vacuole recognisable; cortical granules likely lacking; cytoplasm colourless.

Remarks: Until now, *Apourosomoida* was a small genus comprising two species from highly saline soils in Africa, namely *A. halophila* and *A. natronophila* (Berger 2008). Here I add three "*Cladotricha*" species described by Ruinen (1938) because their cirral pattern agrees basically rather well with that of *A. halophila*, type of the genus. Since the other four species now included in *Apourosomoida* are not described as detailed as the type species, many features (e.g., exact arrangement of frontoventral cirri, origin of certain anlagen) are not known so that their assignment to *Apourosomoida* is not quite certain. Therefore I classify them as species incertae sedis in *Apourosomoida*. The continuance of the three species described by Ruinen (1938) in *Cladotricha* would reduce this genus to a melting pot of halophilous hypotrichs with rather different cirral pattern.

I took over the genus characterisation from Berger (2008) who exclusively based it on the exhaustive description of the type species by Foissner et al. (2002a). *Apourosomoida* differs from *Cladotricha*, inter alia, by the presence of (i) admittedly inconspicuous transverse cirri, (ii) postoral ventral cirri, and (iii) a curious dorsal kinety pattern. The adoral zone is not distinctly gonostomatid in the type species (for detailed review, see Berger 2008, p. 514), *A. variabilis*, and *A. natronophila*. By contrast, the adoral zone of at least *A. kahli* is reminiscent of *Gonostomum* (Fig. 113a). Whether *Cladotricha* and *Apourosomoida* are more or less closely related can only be estimated when the type species of *Cladotricha* is redescribed in detail, and when both type species are analysed with meaningful molecular methods.

Originally, we assigned *Apourosomoida* to the oxytrichids (Foissner et al. 2002a), a classification taken over by Jankowski (2007) and Lynn (2008). However, the Oxytrichidae are – via *Oxytricha granulifera* Foissner & Adam, 1983a, the type species of the whole group – Dorsomarginalia with a fragmentation in kinety 3. Since these features are lacking in *A. halophila*, I removed the present genus from the oxytrichids and classified it (preliminary) as incertae sedis in the Hypotricha (Berger 2008).

Interestingly, no *Cladotricha* species is recorded from Africa whereas at least the type species of *Apourosomoida* and *A. natronophila* have their type localities in this continent, indicating that *Cladotricha* is replaced by *Apourosomoida* in this biogeographic region. Of course, the currently available faunistic data are scanty so that this hypothesis is rather vague.

Foissner et al. (2002a, p. 759) and Berger (2008, p. 515) discussed whether or not *Urosomoida minima* Hemberger, 1985 belongs to *Apourosomoida*. I classified *Urosomoida* Hemberger in Foissner, 1982 in the oxytrichids, assuming that dorsal kinety fragmentation was lost (Berger & Foissner 1997; Berger 1999, p. 76, 345), that is, *Urosomoida* has three bipolar dorsal kineties and a dorsomarginal row. In contrast, now I suppose that this kinety pattern is characteristic for non-oxytrichid dorsomarginalian hypotrichs (Berger 2006a, p. 33; Berger 2008, p. 46). Thus, *Uro-*

somoida and other 18-cirri hypotrichs with such a dorsal infraciliature (e.g., *Urosoma*, some *Oxytricha* species) have to be removed from the oxytrichids (see footnote at molecular data of *Engelmanniella mobilis*). Hemberger (1982, 1985) did not provide an illustration of the dorsal kinety pattern of *U. minima*; in addition, the description is not very thorough because only the number of kineties (three), but not the pattern (e.g., all bipolar? two bipolar and one shortened?) is mentioned. Thus, a detailed estimation of the phylogenetic position of *U. minima* is not possible at the present state of knowledge. Since its habitus and cirral pattern are reminiscent of those of *Apourosomoida*, it is included in the key below. However, the habitat (German garden soil) and the insufficiently known dorsal kinety pattern prevent a classification in the present genus. The reduced number of dorsal kineties and the bipartite adoral zone, however, indicate that *U. minima* is also misclassified in *Urosomoida*. A detailed redescription is needed to estimate the phylogenetic position of this little known species more properly.

Species included in *Apourosomoida* (alphabetically arranged basionyms are given): (1) *Apourosomoida halophila* Foissner, Agatha & Berger, 2002a (type species). Incertae sedis: (2) *Cladotricha elongata* Ruinen, 1938; (3) *Cladotricha kahli* Ruinen, 1938; (4) *Cladotricha variabilis* Ruinen, 1938; (5) *Uroleptus natronophilus* Dietz, 1965.

Key to *Apourosomoida* species and similar species

The following key contains, besides the five species now included in *Apourosomoida*, *Urosomoida minima* and *Erimophrya quadrinucleata*, two rather similar, non-halophilous species from European soils. In addition, you find a link to *Cladotricha*, a relatively little known group of halophilous hypotrichs with one or two long frontoventral rows and lacking postoral ventral cirri. Since some of these species are not described very detailed, the key is rather vague. Note that some species are reviewed in other parts of the monographic series.

1 Long frontoventral row lacking (e.g., Fig. 108e in Berger 2008; Fig. 112a). . . . **2**
- One or two long frontoventral rows present (e.g., Fig. 43a, j, k, 44a, 48g). . . . . *Cladotricha* (p. 235)
2 Macronucleus composed of 2 nodules (Fig. 112a, 113a). **3**
- Macronucleus composed of 4 nodules (e.g., Fig. 113a, 114a). **7**
3 Body length 35–50 µm (Fig. 112a, b in Berger 2008). . . . . *Apourosomoida natronophila* (Berger 2008, p. 530)
- Body length more than 50 µm. **4**
4 One large micronucleus in between macronuclear nodules (Fig. 112a). . . . . *Apourosomoida elongata* (p. 687)
- Nuclear apparatus not as above. **5**
5 Body length:width ratio about 8–9:1 (Fig. 113a). . *Apourosomoida kahli* (p. 689)

- Body length:width ratio about 5:1 (e.g., Fig. 108a in Berger 2008). **6**
6 Right marginal row commences about at level of frontal cirri; 3–6, usually 5 postoral ventral cirri (Fig. 108e, f in Berger 2008). . . . . *Apourosomoida halophila* (Berger 2008, p. 516)
- Right marginal row commences about at level of rearmost frontoventral cirrus; 3 postoral ventral cirri (Fig. 110r in Berger 1999). . . . . *Urosomoida minima* (Berger 1999, p. 366)
7 (2) Inhabits non-saline soils (Fig. 124c, d, 125a–g in Berger 2008). . . . . *Erimophrya quadrinucleata* (Berger 2008, p. 595)
- Inhabits saline to highly saline habitats (Fig. 113a, 114a). 8
8 Usually 6–8 postoral ventral cirri (Fig. 114a). *Apourosomoida variabilis* (p. 690)
- Usually 2 postoral ventral cirri (Fig. 113a). . . . . *Apourosomoida kahli* (p. 689)

Apourosomoida elongata (Ruinen, 1938) comb. nov. (Fig. 112a–c)

1938 ***Cladotricha elongata* nov. spec.** – Ruinen, Zoöl. Meded., Leiden, 20: 253, Fig. 10 (Fig. 112a–c; original description; no formal diagnosis provided and very likely no type material available).
1972 ***Cladotricha elongata* Ruinen, 1938** – Borror, J. Protozool., 19: 18 (generic revision of hypotrichs).
1982 ***Cladotricha elongata* Ruinen, 1938** – Hemberger, Dissertation, p. 220 (revision of hypotrichs).
2001 ***Cladotricha elongata* Ruinen, 1938** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 15 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: No derivation of the name is given in the original description. The species-group name *elongat·us*, *-a*, *-um* (Latin adjective [m; f; n]; elongated, stretched) obviously refers to the elongate body. A neotypification is strongly recommended because (i) the description is not very detailed; (ii) no type material is available; and (iii) no type locality is fixed. In addition, Ruinen did not mention from which population the illustrations are.

Remarks: Borror (1972) accepted all *Cladotricha* species described by Ruinen (1938), but was uncertain about their generic status. According to Hemberger (1982), *C. elongata* and *C. kahli* are not congeneric with *C. koltzowii*, type of *Cladotricha*. He supposed that they either belong to *Perisincirra*[1] or to *Urosomoida* (for review, see Berger 1999, p. 345)[2] because of the postoral ventral cirri. Indeed, the postoral ventral cirri obviously present in *C. elongata* (Fig. 112a), *C. kahli* (Fig. 113a), and *C. variabilis* (Fig. 114a) and the lack of a long frontoventral row support Hemberger's idea that these three species do not belong to *Cladotricha*. Further details on the transfer from *Cladotricha* to *Apourosomoida*, see genus section.

Apourosomoida elongata and *A. kahli* have a very similar habitus, but differ in the nuclear apparatus (two macronuclear nodules with prominent micronucleus in

[1] Later, most of Hemberger's (1982) new *Perisincirra*-species have been validly established in *Hemisincirra* by Hemberger (1985) (for review, see Berger 2008, p. 387).
[2] See p. 553 in present book for a comment on *Urosomoida*.

between vs. two pairs of macronuclear nodules) and the number of large frontal membranelles (two vs. three). Thus, synonymy of these two species is very unlikely. Further studies are needed for a well-founded classification.

Morphology: Body 100–150 µm long, length:width ratio about 13:1, body thus ribbon-shaped, flattened, often helically rolled up; rear body end rounded (Fig. 112a, b). Nuclear apparatus in central body portion; obviously rather conspicuous because composed of two elongate, granulated macronuclear nodules connected by a large (7–9 × 4 µm) micronucleus. Movement and presence/absence of contractile vacuole and cortical granules not mentioned. Some serially arranged food vacuoles.

Adoral zone short, that is, occupies only about 10% of body length; two very large membranelles protruding anteriad (Fig. 112a); Fig. 112b shows the frontal body portion in dorsal view; it is ambiguous whether the five structures marked with a long arrow are (i) the distal portion of the adoral zone, (ii) frontoventral cirri, or most likely (iii) the anterior portion of the right marginal row.

Cirral pattern as in *A. kahli*, according to Ruinen (1938). Specimen illustrated with six cirri arranged along distal portion of adoral zone. Buccal cirrus perhaps lacking. Two postoral cirri arranged in longitudinal row. One (transverse?) cirrus in centre of rear end. Right marginal row composed of 25 cirri and commencing about at level of postoral ventral cirri or close to large membranelles (Fig. 112b). Left marginal row composed of 22 cirri and beginning at level of buccal vertex; rearmost left and right marginal cirrus enlarged and elongated.

Dorsal infraciliature (length and arrangement of bristles; presence/absence of caudal cirri) not described; according to Ruinen (1938, p. 249), *Cladotricha* species (and therefore the present

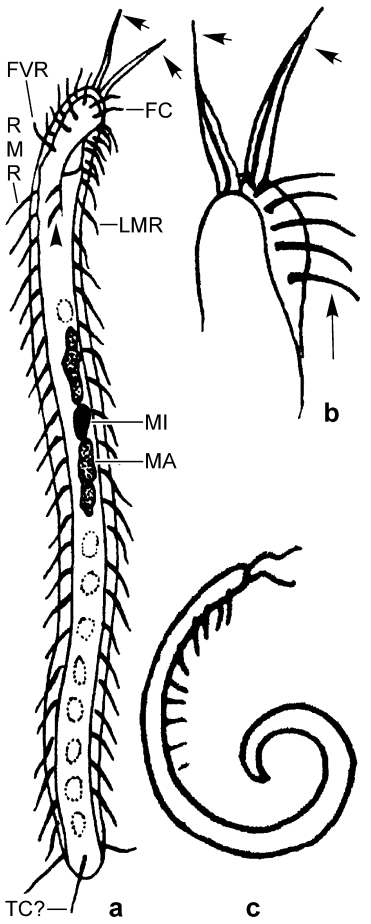

Fig. 112a–c *Apourosomoida elongata* (from Ruinen 1938. From life). **a:** Ventral view of representative specimen showing cirral pattern, nuclear apparatus, and food vacuoles, 100–150 µm. Arrows mark the two large frontal adoral membranelles, arrowhead denotes postoral ventral cirri. **b:** Anterior body end in dorsal view. Short arrows mark the two large frontal adoral membranelles. The correct designation of the cirri marked with long arrow is not known (distal portion of adoral zone? second short frontoventral row? anterior portion of right marginal row?). **c:** Helically wound specimen. FC = left frontal cirrus, FVR = rearmost cirrus of frontoventral row, LMR = left marginal row, MA = rear macronuclear nodule, MI = micronucleus, RMR = anterior end(?) of right marginal row, TC? = transverse cirrus? Page 687.

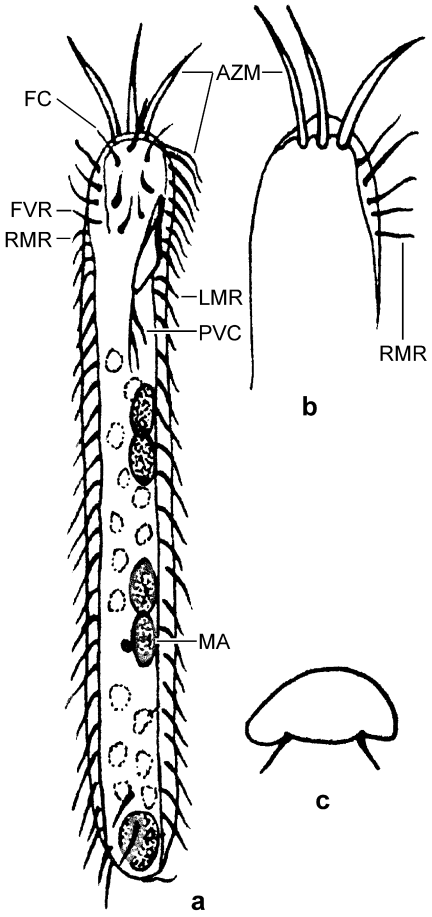

Fig. 113a–c *Apourosomoida kahli* (from Ruinen 1938. From life). **a:** Ventral view of representative specimen, 100–150 µm. The large dotted structure in the rear body portion is likely a defecation vacuole. **b:** Anterior body portion in dorsal view. **c:** Cross-section showing dorsoventral flattening and marginal rows. AZM = adoral zone of membranelles, FC = right frontal cirrus, FVR = frontoventral row, LMR = left marginal row, MA = rearmost macronuclear nodule with micronucleus, PVC = postoral ventral cirri, RMR = right marginal row. Page 689.

species too) have a vestigial or even lacking dorsal ciliature; however, this statement must no be overinterpreted because this part of the infraciliature is very difficult to recognise in detail without protargol impregnation.

Occurrence and ecology: *Apourosomoida elongata* is likely confined to highly saline habitats. Ruinen (1938) found it in two sites, which are far apart and from different biogeographic regions; unfortunately he did not fix one as type locality: saturated solutions from sample(s) from a saline in Setubal, a city about 30 km south-east of Lisbon (Portugal); strongly concentrated solution from "Voigt", which is, according to Ruinen (1938, p. 246), a gypsum or salt lake in southern Australia. Food not known. No further records published.

Apourosomoida kahli (Ruinen, 1938) comb. nov.
(Fig. 113a–c)

1938 ***Cladotricha kahli* nov. spec.** – Ruinen, Zoöl. Meded., Leiden, 20: 253, Fig. 9 (Fig. 113a–c; original description; no formal diagnosis provided and very likely no type material available).
1972 ***Cladotricha kahli* Ruinen, 1938** – Borror, J. Protozool., 19: 18 (generic revision of hypotrichs).
1982 ***Cladotricha kahli* Ruinen, 1938** – Hemberger, Dissertation, p. 220 (revision of hypotrichs).
2001 ***Cladotricha kahli* Ruinen, 1938** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 15 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

Nomenclature: Ruinen (1938) obviously dedicated this species to the great ciliatologist Alfred Kahl (Hamburg), who supervised his study on the saltwater ciliates.

Remarks: Cirral pattern and nuclear apparatus very similar to *Apourosomoida variabilis* and therefore perhaps synonymous with this species. For comments on the classification by Borror (1972) and Hemberger (1982) and separation from *A. elongata*, see *Apourosomoida elongata*.

Morphology: Body length 100–150 µm, length:width ratio about 8–9:1, that is, body broad ribbon-shaped; posterior end rounded. Body ventral flat, dorsal side distinctly vaulted (Fig. 113a, c). Two elongate bipartite (dumbbell-shaped) macronuclear nodules clearly separated from each other in central portion of cell slightly left of midline (whether these are two or four nodules is not quite certain; probably the number is variable); two small, globular micronuclei attached to macronuclear nodules. Presence/absence of contractile vacuole and cortical granules and movement not mentioned. Food vacuoles arranged in two or three rows.

Adoral zone occupies about 21% of body length, gonostomatid; paroral(?) or buccal lip well-developed (Fig. 113a). Three distalmost membranelles enlarged and elongated. Cirral pattern according to Fig. 113a composed of three frontal cirri, two (buccal?) cirri close to buccal lip, two (parabuccal?) cirri behind right frontal cirrus, and four cirri forming short frontoventral row right of parabuccal(?) row. Two postoral cirri about in midline; two cirri roughly in midline of posterior body portion. Right marginal row composed of 33 cirri in specimen illustrated, commences dorsally close to distal end of adoral zone (Fig. 113b), extends along cell margin on ventral side to near cell end; rearmost two or three cirri enlarged, a feature not clearly recognisable in Fig. 113a. Left marginal row composed of about 21 cirri, extends from near buccal vertex to near cell end. Dorsal bristles not recognisable (Ruinen 1938).

Cell division: During the development of the nuclear apparatus, cap-like structures occur sometimes on the anterior end of the two bipartite macronuclear nodules (Ruinen 1938); likely the area behind the replication band. Micronuclei not always recognisable during this process.

Occurrence and ecology: Likely confined to highly saline habitats. *Apourosomoida kahli* was discovered in a 14 per cent NaCl solution from "Voigt", which is, according to Ruinen (1938, p. 246), a gypsum or salt lake in southern Australia. No further records published. Food not known.

Apourosomoida variabilis (Ruinen, 1938) comb. nov.
(Fig. 114a–c, f–m)

1938 ***Cladotricha variabilis* nov. spec.** – Ruinen, Zoöl. Meded., Leiden, 20: 251, Fig. 8 (Fig. 114a–c, f–g, nec Fig. 114d; original description; no formal diagnosis provided and very likely no type material available).

1972 ***Cladotricha variabilis* Ruinen, 1938** – Borror, J. Protozool., 19: 18 (generic revision of hypotrichs).

1979 ***Cladotricha variabilis* Ruinen, 1938** – Borror & Evans, J. Protozool., 26: 52, Fig. 1–5 (Fig. 114h–m; description of Great Salt Lake population and cell division; site were voucher slides deposited not mentioned, perhaps in the University of New Hampshire where Borror worked).

1982 ***Paragastrostyla variabilis* (Ruinen, 1938)** n. comb.[1] – Hemberger, Dissertation[2], p. 203 (revision of hypotrichs).

2001 ***Cladotricha variabilis* Ruinen, 1938** – Berger, Catalogue of ciliate names 1. Hypotrichs, p. 16 (nomenclator containing all basionyms, combinations, and higher taxa of hypotrichs).

2002 ***Cladotricha variabilis* Ruinen, 1938** – Foissner, Agatha & Berger, Denisia, 5: 771, Fig. 166g, i, k–m (Fig. 114a–c, f–g; fixation of Fig. 114a as type of *C. variabilis*).

2008 ***Cladotricha variabilis*** – Berger, Monographiae biol., 88: 517, Fig. 111a–c, e–g (Fig. 114a–c, f–g; revision of *Apourosomoida*).

Nomenclature: No derivation of the name is given in the original description. The species-group name *variabil·is*, *-is*, *-e* (Latin adjective [m; f; n]; variable) obviously alludes to the variable body shape and/or the high variability in general.

Remarks: *Cladotricha variabilis* sensu Ruinen (1938) is very likely a mixture of two species (Foissner et al. 2002a). Ruinen studied specimens from two sites (Setubal in Portugal and Marion Bay in Australia), but unfortunately did not fix one site as type locality[3]. In addition, he did not mention which illustration refers to which population. Thus, neotypification is unavoidable to solve this rather tricky situation (see also remarks). As a first step, Foissner et al. (2002a) fixed the specimen shown in Fig. 114a as "type" of *C. variabilis*, and that shown in Fig. 114d as supposed synonym of the type species *Apourosomoida halophila* (for review, see Berger 2008, p. 516).

Foissner et al. (2002a, p. 760, 771) supposed that *C. variabilis* sensu Borror & Evans (1979; Fig. 114h–m) from the Great Salt Lake neither belongs to *Cladotricha* nor to *Apourosomoida* because of differences in morphology (postoral ventral cirri, transverse cirri) and ontogenesis (e.g., number of anlagen), and that it is not conspecific with *C. variabilis* sensu Ruinen (1938, Fig. 114a) because of a different number of macronuclear nodules (two vs. four). Regrettably, the actual situation does not yet allow a serious rearrangement, that is, a detailed redescription including neotypification of *A. variabilis* should be awaited. As is usual for such an unsatisfactory situation I keep the descriptions of the populations separate.

Apourosomoida variabilis has two important features in common with *A. elongata* (Fig. 112a) and *A. kahli* (Fig. 113a), namely postoral ventral cirri and a lacking

[1] This name is disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3).

[2] According to the ICZN (1964), dissertations are not explicitly mentioned under Article 9, which describes all those acts that do not constitute a publication within the meaning of the Code. Thus, Hemberger's (1982) thesis, for which the ICZN (1964) has to be applied, could possibly also be considered as nomenclaturally valid work. Unfortunately, the situation is rather complicated and almost each thesis would need a detailed analysis whether or not it meets the requirements of publication (P. Tubbs, ICZN, Natural History Museum, London, pers. comm.). Thus, I do not accept Hemberger (1982) as combining author. However, I include the thesis in the list of synonyms because it is one of the most important papers on hypotrichs since Kahl (1932). To avoid nomenclatural problems each new name or combination mentioned by Hemberger (1982) is individually disclaimed for nomenclatural purposes.

[3] Earlier we incorrectly assumed that *C. variabilis* is from Australia (Foissner et al. 2002a, p. 771).

long frontoventral row. Further details on the transfer from *Cladotricha* to *Apourosomoida*, see genus section.

Hemberger (1982) transferred *C. variabilis* to *Paragastrostyla*, an act which is (very likely) nomenclaturally invalid (see footnotes at list of synonyms above and Berger 2006a, p. 617). *Paragastrostyla* Hemberger, 1985 is a urostyloid and therefore *C. variabilis* was not included in this genus by Berger (2006a, p. 617).

Strongylidium arenicolum Dragesco, 1953, type of *Stenotricha* Jankowski, 1978, is very similar to *C. variabilis* according to Hemberger (1982) because they agree in the general cirral pattern and the nuclear apparatus. However, there are some differences (e.g., shape and structure of adoral zone, size of transverse cirri) strongly indicating that they are not synonymous (see *Stenotricha*, p. 680). Both species have to be redescribed in detail for a more detailed estimation of the phylogenetic relationship.

Morphology: Ruinen (1938) very likely confounded two populations, one of which (Fig. 114d) is perhaps identical with *A. halophila* (Berger 2008, p. 516). Thus, the description of the cirral pattern of *A. variabilis* is mainly based on the relevant illustrations (Fig. 114a, b, f, g).

Population studied by Ruinen (1938): Body length 100–150 µm, length:width ratio of specimen shown in Fig. 114a about 4.7:1. Body outline fusiform, rear end blunt to tapered. Degenerated specimens wedge-shaped (Fig. 114c). Specimen illustrated with two pairs of macronuclear nodules arranged slightly right of midline; to each distalmost nodule one micronucleus attached; micronuclei 5 × 2 µm (Fig. 114a). Nuclear figures shown in Fig. 114e likely belong to *A. halophila*, which has two macronuclear nodules. Contractile vacuole and cortical granules neither mentioned nor illustrated, indicating that both structures are lacking. Movement not described.

Adoral zone distinctly bipartite in three large distal membranelles inserted dorsally and extending anteriad, and a main part exclusively arranged on ventral side. Undulating membranes not described in detail[1].

Three frontal cirri, one buccal(?) cirrus, one parabuccal(?) cirrus, and one short frontoventral row composed of about five cirri left of anterior portion of right marginal row. One postoral row usually composed of six cirri (Fig. 114a, b); left of anterior part of this row two (Fig. 114a), one (Fig. 114g), or no (Fig. 114c) cirrus present (specimens with no cirrus left of anterior portion of postoral row likely belong to the *Apourosomoida halophila*-like population). Specimen shown in Fig. 114a with two longitudinally arranged pairs of cirri in midline of posterior body third and two pairs of enlarged cirri on rear cell end, one right dorsolaterally, the other left ventrolaterally; whether these are transverse, and/or caudal, and/or marginal cirri is actually not known. Right marginal row commences on dorsal side at distal end of adoral

[1] Ruinen (1938) writes that the undulating membrane is somewhat more distinct than in the other species. However, it is unclear whether this vague statement applies to the population shown in Fig. 114a or to that shown in Fig. 114d which is perhaps identical with *A. halophila*. Perhaps he confused buccal lip and paroral.

zone, main part, however, extends on ventral side, terminates distinctly ahead of rear cell end. Left row begins left of buccal vertex, ends subterminally. Dorsal infraciliature (length and arrangement of bristles, caudal cirri present/absent) not known.

Great Salt Lake population studied by Borror & Evans (1979): Body size not mentioned, specimen illustrated about 125 µm long (Fig. 114h). Body roughly drop-shaped in life (?); supple; usually contorted in life, with right marginal row normally twisted about 180°. Nuclear apparatus composed of two relatively large macronuclear globules, each associated with an ellipsoidal micronucleus. Cortical granules lacking. Adoral zone composed of about 20–25 membranelles, occupies 30% of body length in specimen illustrated (Fig. 114h). Buccal cavity about 30 µm long, posterior fourth narrow and cylindrical; "most of paroral apparatus is deep in this posterior section of the buccal cavity" according to Borror & Evans (1979). Variability of cirral pattern rather high. Four cirri form curved pseudorow along anterior cell end (Fig. 114h), likely three ordinary frontal cirri and a parabuccal cirrus; second arching pseudorow commencing about at anterior end of undulating membranes, terminating near rear end of short frontoventral row; both pseudorows likely composed of 5–8 cirri. Frontoventral row left and parallel to anterior portion of right marginal row, composed of 4–7 cirri. Postoral row composed of 5–8 cirri, with an additional row of 1–4 (sometimes zero) cirri left of anterior portion of postoral row. According to Borror & Evans (1979), each frontal cirrus composed of 4–6 cilia (it is unclear whether this specification refers only to the true frontal cirri or all cirri in the frontal and/or postoral region). Right marginal row of specimen illustrated composed of 23 cirri (Fig. 114h; anterior cirri on dorsal side [cp. Fig. 114b] obviously not illustrated). Left marginal row commences left of buccal vertex. Dorsal infraciliature not illustrated in detail, but described at some length. Since the description is cryptic in some cases it is given word for word: "The dorsal ciliature consists of a short inconspicuous oblique row of about three cilia adjacent and dorsal to the anterior terminus of the right marginal cirri; an oblique helical "mid-dorsal" series of about 10–12 cilia, the last two of which are differentiated into caudal cirri with about two cilia apiece and 1–2 additional cilia; and a terminal caudal cirrus immediately to the observer's left of the longer row". I suppose that the pattern is very similar to that of *Apourosomoida halophila* (see Fig. 108f in Berger 2008). Length of bristles not mentioned, according to Fig. 114h about 8–10 µm. Caudal cirri stiff and vibratile, protrude nearly vertically.

Cell division (Fig. 114i–m): Borror & Evans (1979) described the cell division of the Great Salt Lake population. They provided five (not very detailed) illustrations and a lengthy description (for summary, see Foissner 1996, p. 105).

Morphogenesis commences with the parakinetal formation of an oral primordium originating from the postoral cirral row (Fig. 114i, j). In a middle stage the new adoral zone, the undulating membrane anlage, and five frontal-ventral cirri anlagen are present in the opisthe (Fig. 114k). In the proter, the cirri forming the rear bow of frontal cirri and the rear part of the short frontoventral row have modified to anlagen. In late dividers, in total six anlagen (I–VI) are present in both the proter

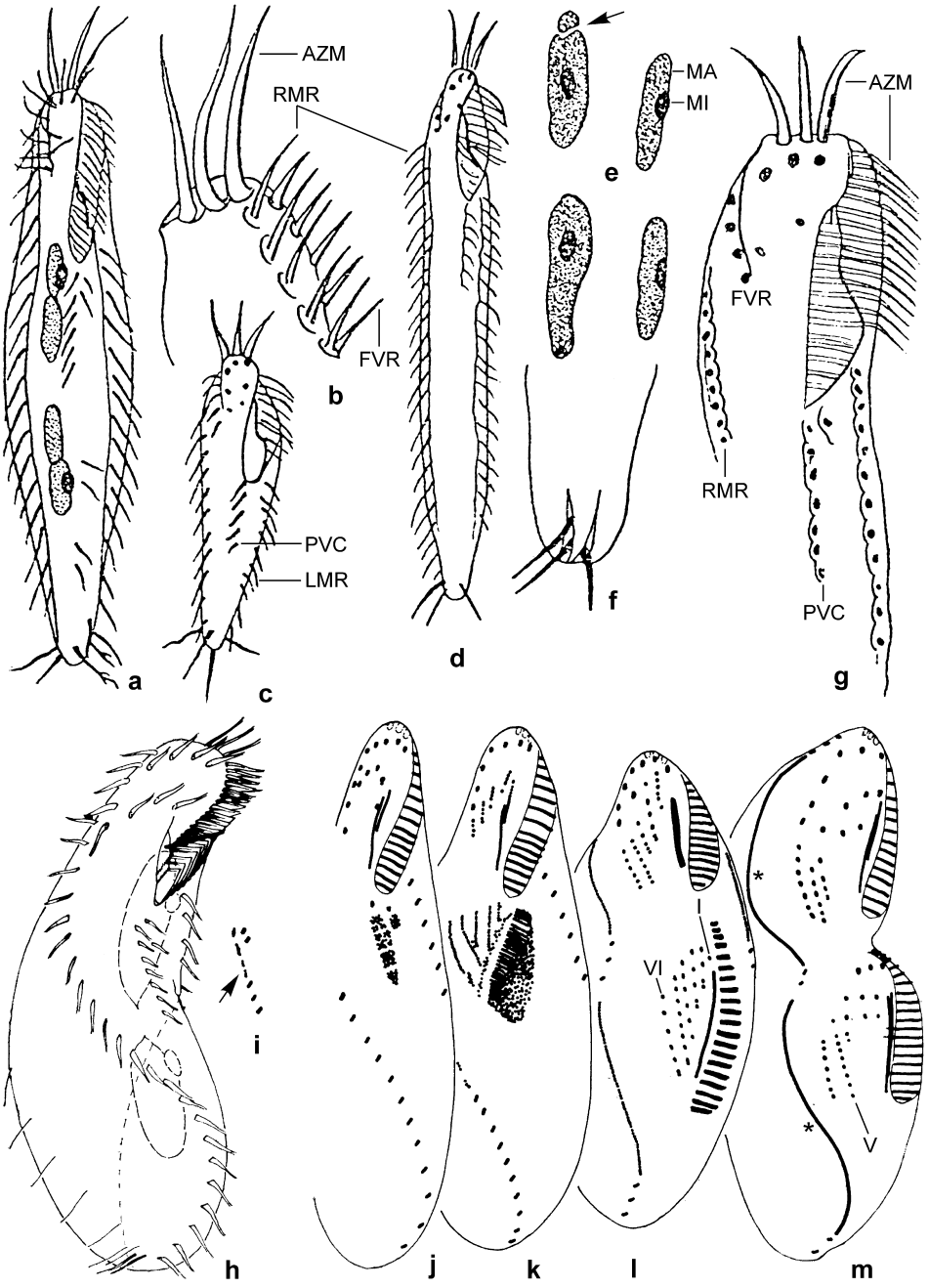

Fig. 114a–m "*Apourosomoida variabilis*" (a–g, from Ruinen 1938; h–m, from Borror & Evans 1979. a–g, from life; h–m, probably protargol impregnation). Note: For detailed explanation of problems (likely two species mixed, type locality not fixed), see text. **a:** Ventral view of representative specimen, 100–150 µm. This quadrinucleata specimen/population was fixed as type of *C. variabilis* by Foissner et al. (2002a). **b:** Anterior body end in dorsal view. **c:** Degenerated specimen. **d:** Specimen/population perhaps identical with

and the opisthe (Fig. 114l, m). The postoral cirri of the proter develop from anlagen IV and V. The left frontal cirrus and the undulating membranes originate, as is usual, from anlage I which is formed from the realigned parental undulating membranes. The short frontoventral row is formed by the rightmost anlage (VI) and is therefore very likely homologous with the frontoterminal cirri of other hypotrichs. The proter inherits the parental adoral zone.

The marginal rows of the proter and the opisthe originate in the ordinary manner, that is, by intrakinetal proliferation at two levels. The anterior portion of the right marginal rows extends dorsally while the posterior portion of the row is twisted ventrad nearly 180°.

Unfortunately, Borror & Evans (1979) did not illustrate the dorsal morphogenesis, which proceeds rather unusual, according to the description. The short row right of the anterior portion of the long median row originates in proter and opisthe independent of parental dorsal bristles; perhaps it is a dorsomarginal kinety. At two positions on the median row arise anlagen with about 10–15 close-set basal bodies. While the remainder of the parental bristles dedifferentiate, the posterior half of each anlage separates from the rest of the streak, and comes to lie to the "observer's left"[1] of the original row. As the cell elongates, the anlagen elongate also, and the bristles become more widely spaced. The bristles of the longer anlage form the main (median) dorsal kinety and 1–2 caudal cirri; the bristles of the other anlage form 1–2 additional posterior bristles and a caudal cirrus. The process is obviously relatively complicated, but the presence of caudal cirri on both kineties (left and median) indicates that it is not homologous with the ordinary oxytrichid kinety fragmentation. I suppose that it is very similar or even identical with that described for the type species of *Apourosomoida* (Foissner et al. 2002a; Berger 2008, p. 528).

Occurrence and ecology: *Apourosomoida variabilis* is likely confined to highly saline waters/habitats. Note that the populations described above are perhaps not conspecific. In addition, Ruinen (1938) studied populations from two sites, but did not fix one as type locality (see remarks). One population is from sample(s) from a saline in Setubal, a city about 30 km south-east of Lisbon (Portugal), the other is from the Marion Bay, about 100 km west of Adelaide, Australia. The samples had a

← *Apourosomoida halophila* (see remarks). **e:** Nuclear apparatus of two specimens (of the bimacronucleate *A. halophila*). Arrow marks replication band. **f:** Rear body portion showing three caudal cirri or two caudal cirri and one transverse cirrus as in *A. halophila*. **g:** Ventral view of anterior body portion. Note the single postoral ventral cirrus left of the anterior portion of the postoral row, indicating that this specimen belongs to *A. variabilis*. **h:** Interphasic specimen of Great Salt Lake population, 125 µm. **i–m:** Cell division. Arrow in (i) marks first sign of oral primordium formation in postoral row. Asterisks in (m) mark right marginal row anlagen. Anlage V forms likely the postoral row, anlage VI probably forms the short frontoventral row. Note that *A. variabilis* produces six frontal-ventral cirri anlagen whereas *A. halophila* forms only five. Further details, see text. AZM = adoral zone of membranelles, FVR = frontoventral row, LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, PVC = postoral ventral cirri, RMR = right marginal row, I, V, VI = frontoventral cirri anlagen. Page 690.

[1] This likely means next to the left marginal row.

NaCl concentration of 60–180‰. The *Cladotricha* species studied by Borror & Evans (1979, p. 52) are from samples collected along the southern and eastern beaches of the Great Salt Lake[1] (Utah, USA), where the salt concentration varied from 200‰ to 10‰ near the mouth of the Jordan River; *Cladotricha koltzowii* and *Apourosomoida variabilis* were tolerant to rapid salinity changes, and reacted normally to salt concentrations as low as 20‰. Post et al. (1983) found *Cladotricha* species (including *C. variabilis*) in the Hutt Lagoon (28°11' S 114°15'E), about 600 km north of Perth, Australia (see also Hauer & Rogerson 2005, p. 525). *Apourosomoida variabilis* is a voracious consumer of *Dunaliella*, according to Post et al. (1983).

[1] Foissner et al. (2002a, p. 771) mistakenly wrote that Borror & Evans (1979) found *C. variabilis* in New Hampshire, USA.

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Systematic Index

The index contains all names of hypotrichous ciliates mentioned in the book, including vernacular names for example, kahliellids (designations as, for example, "spirotrichous ciliates" are mentioned under the corresponding vernacular name, that is, spirotrichs in example); food organisms, other ciliates, and other organisms are usually not included, except for those mentioned in the general section. The index is two-sided, that is, species appear both with the genus-group name first (for example, *Gonostomum affine*) and with the species-group name first (*affine, Gonostomum*). Valid (in my judgement) species and genera are in ***boldface italics*** print. Valid taxa not revised in the present book, invalid taxa, junior homonyms, synonyms, outdated combinations, incorrect spellings, and nomina nuda are given in italics. The scientific name of a subgenus, when used with a binomen or trinomen, must be interpolated in parentheses between the genus-group name and the species-group name (ICZN 1999, Article 6.1). In the following index, these parentheses are omitted to simplify electronic sorting. Thus, the name *Paragonostomum (Bigonostomum) multinucleatum* is listed as *Paragonostomum Bigonostomum multinucleatum*. Note that this name is also listed under "*Bigonostomum multinucleatum, Paragonostomum*" and "*multinucleatum, Paragonostomum Bigonostomum*". Suprageneric taxa are represented in normal type, valid ones revised in the present review in **boldface**. **Boldface page number** indicates the location of a valid taxon in the systematic section. "T" indicates the location of the table with the morphometric characterisation; "K" marks the page where a taxon is mentioned in a key (note that some taxa are mentioned two times in one key or in two different keys). **Boldface page number** plus "**K**" marks the page where a key begins (e.g., Key to *Orthoamphisiella* species). Homonyms (e.g., *Uroleptus kahli* Grolière, 1975 and *Uroleptus kahli* Buitkamp, 1977 or *Meseres* Schewiakoff, 1892 and *Meseres* Ludwig, 1893) are not indexed separately.

Table Index