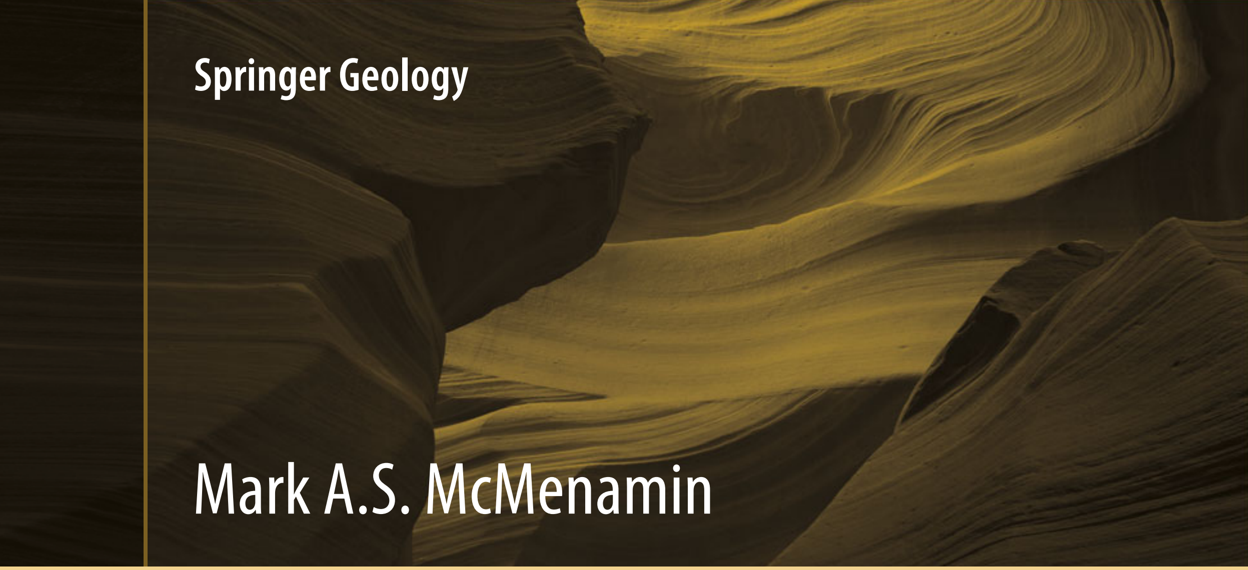

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Mark A.S. McMenamin

Dynamic Paleontology

Using Quantification and Other Tools to Decipher the History of Life

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To David Raup (1933–2015)

Preface

It has been said that scientific knowledge is built on the ruins of failed hypotheses. The real work of constructing science, however, is in the careful selection of tractable problems, solving them, and then applying their solutions to other, more difficult problems. Challenging problems cannot be solved without extensive preliminary groundwork. Peter Medawar once said that "science is the art of the soluble," and an important part of the art of science lies in properly laying the groundwork.

The goal of this book is to introduce the art of the soluble as applied to paleontology. By means of more than a dozen case studies, or critical research topics, I hope to demonstrate how asking the right questions can produce not only correct answers to the original problems but can also provide fresh insight into conundrums that might otherwise remain refractory of solution. I have selected these particular cases because they interact with each other in fruitful ways. Useful interactions between investigations generate synergy that can be used to pry open some of the toughest secrets of the natural world.

A great strength of paleontology is that it can draw from temporal–historical sources of information that are not as frequently utilized in cognate sciences. This gives paleontology a multi-dimensional quality that allows the careful researcher to triangulate research investigations through time, as for example by asking what relationship characteristics of the Proterozoic might have to features of the Mesozoic, and what the Cambrian might tell us about paleobiological events occurring before the Cambrian. Universal, actualistic physical principles can be addressed by paleontology as well, because the stratigraphic record itself provides an answer key with every slab of rock and each fossil. A common slab of limestone with trilobite fossils is the answer to some important paleontological question. Researchers need to know how to ask the right question. A potentially fruitful tutorial for that skill is study of the cases where the *Dynamic Paleontology* approach has been most successful.

Dynamic Paleontology wades into controversy at times. Passions run high on many issues. This is good for the science as it focuses attention on the most critical topics. The flip side of the coin is that *Dynamic Paleontology* methodology is not foolproof. Paleontology is by its very nature an error–prone process. Making honest mistakes is unmistakably a key part of the process. There is general agreement among paleontologists that unless you make the occasional mistake, such as Simon Conway Morris reconstructing *Hallucigenia* upside down or Louis Agassiz misinterpreting the aetosaur *Stagonolepis* as a fish, then you are not doing your job as a paleontologist. In the self–correcting scientific process, what remains after vigorous scrutiny is pure gold. *Dynamic Paleontology* aspires to accelerate this process, and it is my conviction that we can learn things about the history of life using this approach that cannot be learned in any other way.

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Contents

Chapter 1
Scleritome

> *All great deeds and all great thoughts have ridiculous beginnings.*
>
> Albert Camus (1913–1960)

Abstract What controls the geometry of the scleritome mosaic? Does it have any relationship to the rapid, major morphological changes? Morphogenetic field analysis helps to explain, by means of laws of morphogenetic evolution, the geometrical patterning of sclerites in a scleritome. Many cases of convergent evolution may thus be viewed as torologous relationships because of the underlying toroidal shape of the scleritome grid. Rapid transformation of morphogenetic fields played a role in the process that led to the appearance new phyla during the Cambrian Explosion.

Paleontology spans the discovery of new fossils to analyses of long lists of taxa indexed by age, geographic distribution and affinity. The goal of these efforts is always the same, namely, to discern the patterns and processes at work that led to the construction of our biosphere. Some approaches in paleontology work better than others. The goal of this book, by means of a series of case studies, is to identify and refine the best approaches as models for solving critical problems in Earth science. Events that occurred a half billion or more years ago require careful analysis if we hope to discern what actually happened and why these events matter. Of particular interest, especially for students, are the best practices for experimental design and best methods for linking one discipline to another for the purpose of solving what might be otherwise intractable problems. Successful efforts will generate new and reliable information about the history of life, and will provide access to information that might be difficult, or impossible, to obtain by any other method.

Previous writers in this field have attempted to compass the entire invertebrate fossil record. Comprehensive texts have ranged from wide-ranging American (Tasch 1980) to more focused British (Clarkson 1998) approaches. Such comprehensive treatment is beyond the scope of this book. My goal is to identify and

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describe a limited set of key but discrete examples that provide exemplars of the *Dynamic Paleontology* approach.

There is worrying trend in biological sciences for publication of complex quantitative results that are either, *first*, poorly constructed in terms of their underlying assumptions, or *second*, biased (unconsciously or otherwise) in the direction of what appears to be a foregone conclusion. Many studies are swayed by the influence of powerful paradigms, and their science suffers as a result. František Baluška laments the ascendency of ossified conventional thinking in science, commenting that the "situation is now out of control. Science should be free. It is not free at the moment." The problem with conventional thought in science has been recognized for over a century—Dwight (1911) called it "sham science." Difficulties recently thrown into high relief are now crying out for resolution (McMenamin 2013). We should care about this if we value the integrity of science as an intellectual pursuit. There are, however, encouraging signs on the horizon. The return of biological structuralism (Denton 2013) heralds a new and improved approach to the biological sciences.

Errors of the first type are of considerable concern. Paleontological investigations based on database manipulation can introduce various errors, and investigators must proceed with caution (Emig et al. 2015). It is more than a mere matter of personal taste that the most important questions in paleontology are not solved by database manipulation, but rather by careful observation and interpretation of singular sites. This is certainly not meant to denigrate the emerging science of paleoinformatics, an important new development where paleontological databases become increasingly available on the Internet. Nevertheless, our work must always focus on a search for causal mechanism—perhaps it would be better to say causal agency. In a recent example from the biological sciences, the aetiology of Alzheimer's disease was quite mysterious until fungal brain infections were discovered in Alzheimer's patients (Pisa et al. 2015). This is a concrete explanation, very different from the concept that Alzheimer's is caused by some kind of progressive deterioration due to toxics, etc., and best handled by statistical treatment of the epidemological data.

Paleontology conducted as a model analytical science requires maintaining a rigorous distinction between concepts of continuous change and discontinuous change. As in the distinction between digital and analog, the results of the two tempos can be similar to the point of being indistinguishable. Nevertheless, the basis of signal transmission is fundamentally different. As in both analog and digital technology, the task at hand in paleontology is to improve the signal-to-noise ratio.

Some distinctions involve a change in state, as for example the transition from laminar flow to turbulent flow. Consider the transition from low flow regime bedforms to high flow regime bedforms in the deposition of layered sediments, where there is a sudden change in the character of the sediment-water interface with increasing current speed. Biological systems frequently manifest abrupt changes in state. It is important to discern differences in both fundamental process and in system state values (such as evolutionary grade). Only then may we fruitfully address pressing questions, such as those concerning the origins of animal behaviors or the suite of factors that control the geochemistry of the biosphere. We might inquire whether our understanding of the habits of an ancient organism depends "on being able to distinguish behavior based on internal or external representations of the environment, with the implication that only organisms with a complex nervous system would be capable of producing the latter" (Budd 2015).

A familiar example will serve below as our first case study. Goose bumps are known as *cutis anserina* or horripilation. The reflex that causes goose bumps is called piloerection. The term horripilation is etymologically derived from Latin *horrere*, which means both "to bristle" and "to be horrified," from whence the English word "horror." The goose bump phenomenon in humans is associated with a wide range of intense emotions, including awe, fear and pleasure. The artist who can trigger this reflex has connected with his or her audience in a meaningful way. Goose bumps, along with development of tears in the eyes and blushing, are considered to be among the most important physiological manifestations of our emotional lives.

What is the origin of goose pimples or goose flesh? Charles Darwin (1872) saw goose bumps as a vestigial reflex derived from our hairy ancestors. Arrector pilli muscular contractions fluff the fur and can make an animal appear larger. The reflex can also enhance the insulating qualities of fur, expanding its ability to trap and retain air warmed by body heat. The retention and maintenance of this apparently vestigial reflex in humans is puzzling. The bump effect is still strong for us but we lack thick body hair that could make us appear larger or keep us warm. With porcupines, piloerection has an obvious function—it brings the quills into defensive position. But for humans the function, if any, is much less clear.

In a scientific spoof that was published in the *Annals of Improbable Research*, Woods (2015) asserted (note carefully the names of the three 'authors') that "three Italian researchers, Capelli, Ricciuto, and Pelato, proposed the Sbaglio Theorem… The principle describes the volume which hair occupies on the head as a function of the degree of spiral. When no spiral is present, the hair grows straight out of the head and occupies maximum volume. As the degree of spiral increases, the volume decreases as the hair forms an orderly matted pattern."

Woods' theorem, although facetious, nevertheless should be elevated to a *law* of morphogenetic evolution. Why must we do this? It is worthwhile investing in a search for laws of nature? Haught (2015) recommends that we "abandon the culturally conditioned juridical metaphor of 'law' when we speak of the invariant principles [of the cosmos]." Haught wants to substitute the metaphors "drama" and "grammatical rules" in place of "mechanism" and "laws of nature." The distinction is largely semantic, although Haught does seem to be trying to distance himself (unwisely in my opinion) from the broader implications of the existence of natural law. Kauffman (1993) argues that the order we see in nature casts "an image of underlying law over biology (p. 644)." Even Huxley (1924) maintained that "education is the instruction of the intellect in the laws of Nature." Whether we call them natural laws or the grammatical rules of nature, we certainly can discern at least some of the fundamental rules in nature and use these discoveries to our advantage. Indeed, is this not the fundamental impulse driving scientific research and investigation?

Woods' (2015) spoof theorem, freshly promoted and expanded, reads here as Sbaglio's Law:

> Changing the orientation of field vectors controlling the position of surface ornamentation can alter surface body form. Altering these same field vectors can *also* fundamentally alter actual body form (baüplan).

Let's now proceed to a "proof of the spoof." Exactly how might altering field vectors (such as the hairs on the crown of someone's head) cause a profound shift in body form, when it merely changes the orientation of surface vectors controlling the position of hairs, scales, spines, etc.? Fluffing may make the animal appear bigger or keep it warmer, but this constitutes no fundamental change to body form. Could this not be merely a self-organized transition from aster form (straight-out hair) to vortex form (spiral cowlick)? If 'self-organization' itself is beholden to laws of form, then the term simply means obeying the laws of nature.

How *can* field vectors alter body form? To begin to answer this question, let's turn to paleontology and consider the early fossil record of the Phylum Echinodermata (starfish, sea urchins, brittle stars, crinoids, sea cucumbers, etc.). We will begin with consideration of a very strange group of echinoderms (the edrioasteroids) in preparation for discussion of an even stranger group of echinoderms (the helicoplacoids). This is an important matter to consider because echinoderms make an abrupt appearance during the Cambrian Explosion. In a subsequent chapter we will consider just how abrupt that appearance actually was. A crucial question has intrigued and inspired paleontologists for over a century. Assuming it occurs at all, what causes rapid, major morphological change?

The early record of echinoderms provides critical clues. Phylum Echinodermata is defined by the presence of calcite skeletal plates formed by a porous monocrystalline structure known as stereom (Zamora et al. 2012). Under the scanning electron microscope, stereom looks like Swiss cheese with a lot of holes, or like foam with big pores. The stereom skeleton differs from many other types of shell because of the absence of collagenous matrix (Kline and Currey 1970; Okazaki 1970). In spite of its complex internal structure, each stereom plate in the echinoderm skeleton consists of a single crystal of calcite. The c-axis of each crystal has a unique orientation, usually perpendicular to the outer surface of the animal. For example, in a sea urchin spine, the c-axis of the stereom is coincident with the long axis of the spine.

Echinoderm fossils are easily recognizable in the fossil record owing to the unique nature of their most preservable parts, their stereom plates. No other organism has this type of skeleton. In life, the pores of stereom are filled with living tissue, rendering echinoderm plates essentially intermediate between external skeleton (e.g., external plates) and internal skeleton (porous with interstitial living tissue as in bone).

Paleontologists in the 1970s began to ask increasingly urgent questions about the earliest history of echinoderms, particularly as regards their apparent abrupt appearance and their putative Precambrian ancestry. Ubaghs (1975) wrote: "Such an early appearance of the major groups of echinoderms, coupled with the astonishing diversity and high degree of specialization shown by the oldest known representatives of the phylum, indicates that the common ancestor and the initial phases in the history of these animals certainly must be traced back to Precambrian times. Consequently, at present paleontology cannot furnish direct evidence bearing on the problem of the origins and relationships of echinoderms, nor on the manner in which their essential features were acquired." This was essentially a restatement of the Cambrian Explosion problem, well known to Charles Darwin and Charles Walcott, namely: Why are there no apparent fossil ancestors of the myriad groups of complex animals that appear at the beginning of the Cambrian?

We can indeed find fossils of the ancestral state of echinoderms, just as Ubaghs predicted. The problem, however, and this highlights the Cambrian Explosion problem and in fact makes it considerably worse, is that these are not Precambrian fossils but Early Cambrian fossils. The first true echinoderm fossils are Early Cambrian in age. Nor are the putative ancestral forms the oldest, but rather they appear stratigraphically after the first echinoderm fossils. This sets the ordinary Darwinian expectation on its ends.

The enigmatic metazoan fossil *Cotyledion tylodes* was first described from the Early Cambrian Chengjiang lagerstätte in 1999. It is a stalked metazoan that lacks confident assignment to phylum. Although it somewhat resembles a stalked echinoderm such as a crinoid or blastoid, a possible echinoderm affinity was rejected in favor of interpreting the animal as a cnidarian polyp (Clausen et al. 2010). Zhang et al. (2013) reinterpreted *Cotyledion* as a stem group entoproct. The higher taxonomic position of *Cotyledion* is thus hotly debated, with no consensus on whether it is a deuterostome or lophotrochozoan, or even a diploblast or a triploblast.

Comparison between the stem sclerites of *Cotyledion* and gogiid eocrinoids such as *Gogia* shows a strong similarity that bespeaks common ancestry (Sprinkle and Collins 2006). *Lyrocystis reesei* has a stalk covered with oval platelets with concentric ridges. *Cotyledion* has this same pattern of stalk sclerites with concentric ridges (Fig. 1.1). Zhang et al. (2013) refer to these as "concentric lamellae," but it

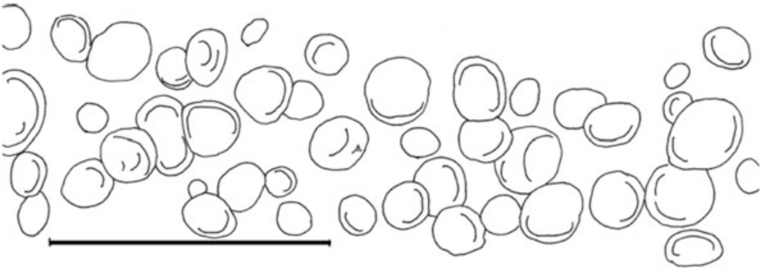

Fig. 1.1 Stem region of the stem-group echinoderm *Cotyledion tyloides*. Note oval stem sclerites with marginal borders. Sketch based on Zhang et al. (2013), their Fig. 1.3. Scale bar = 2 mm

seems quite clear that the structures are homologous to the ridges of the stalk sclerites as seen in *Lyrocystis*. Thus, *Cotyledion* may be assigned to the Deuterostomia as a stem group representative of the Echinodermata. This insight boosts the paleontological signal-to-noise ratio.

The stem similarities are quite apparent when comparing the stem of *Cotyledion* with that of the well-known gogiid eocrinoid *Gogia spiralis* (Fig. 1.2). A concentric ridge is clearly visible on one of the sclerites covering the stem of the eocrinoid (Fig. 1.3). The pattern of stem sclerites in *G. spiralis* is precisely what one would expect if the stem sclerites of *Cotyledion* were to become more heavily mineralized and more crowded on the stem. The slightly crowded effect seen in Fig. 1.2 may be a result of post-mortem contraction of the stem. By comparison, note that the stem of *Cotyledion* shown in Fig. 1.1 appears to be relatively distended or stretched out, as

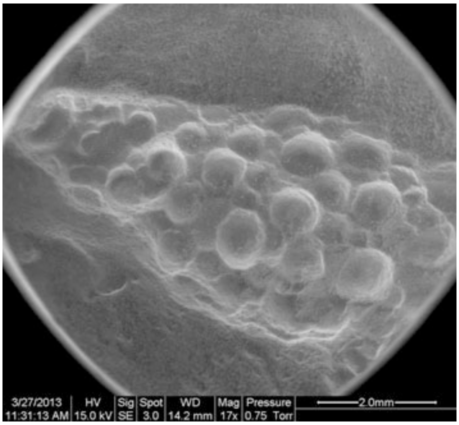

Fig. 1.2 *Gogia spiralis* Robinson, 1965 from the Wheeler Formation, Willard County, Utah. Scanning electron photomicrograph showing sclerites covering the stem of *G. spiralis*. Note concentric ridge on the sclerite close to the center of the image. Scale bar = 2.0 mm

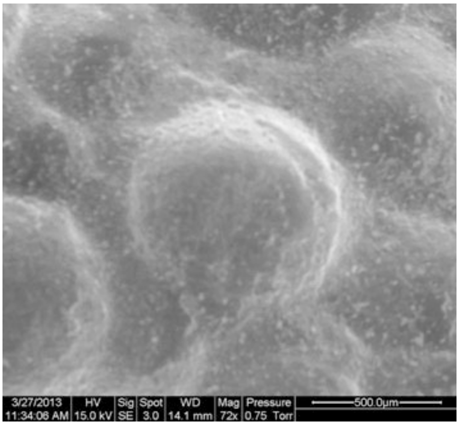

Fig. 1.3 Enlarged view of centrally-located stem sclerite in *Gogia spiralis*. Scale bar = 500 μ

shown by separation of the sclerites. Once these taphonomic peculiarities are accounted for, the *Cotyledion* and *Gogia* stems are quite similar.

There remains a problem with the timing of the first appearance of *Cotyledion tyloides*. Its fossils are the approximately the same age, or even younger, than the first true echinoderm fossils with stereom plates. If the *Cotyledion* fossils had been found in, say, Ediacaran strata, then the traditional expectation as expressed by Ubaghs (1975) would have been satisfied, namely, the soft-bodied ancestor would occur stratigraphically well before the biomineralized descendant. As most of the Ediacaran fossils are soft-bodied, there is certainly no inherent taphonomic reason why *Cotyledion* could not have been preserved in Proterozoic strata.

But this is not what we see in the fossil record. In a case of what has been called phylogenetic telescoping (Conway Morris 2006), the putative ancestors appear at the same time or even *before* the putative descendants. The Lower Cambrian fossil record is rife with examples of phylogenetic telescoping, thus *Cotyledion* by no means represents an isolated case.

A common assumption is that asymmetrical echinoderms, that is, those with spiral or asymmetric body forms, preceded and were ancestral to pentameral echinoderms (Smith and Zamora 2013). Pentameral or five-fold radial echinoderms are characterized by having five ambulacra (food grooves), arranged in a 2-1-2 pattern, that is, one ambulacrum and two branched ambulacral pairs. Under this assumption, spiral/asymmetrical echinoderms such as *Helicoplacus* were precursors to the modern 2-1-2 echinoderms. Similar to the putative *Cotyledion*-to-*Gogia* progression, the *Helicoplacus*-to-pentameral echinoderm sequence is a tempting potential match to Darwinian expectations. Once again, however, the fossil record does not satisfy this expectation.

With regard to fairly complete specimens, Zamora et al. (2013) note that “gogiid eocrinoids and edrioasteroids are consistently the first to appear in the fossil record across all regions.” Interestingly, in this paper, rhombiferans are included as Cambrian taxa—they earlier had been reported to first appear in the Ordovician. The earliest well-mineralized skeletons of echinoderms are known from disarticulated stereom plates. Curiously, one of these fossils shows the ambulacral bifurcation, indicating that the echinoderm to which this plate belonged was of the 2-1-2 type. Here is another case of phylogenetic telescoping, in which the crown group appears before the putative stem group (spiral echinoderms such as *Helicoplacus*).

It is possible to reconstruct this earliest known echinoderm, here named *Sprincrinus inflatus* n. gen. n. sp. The complete reconstruction of the *Sprincrinus* skeleton (Fig. 1.4) is derived from analysis of isolated plates that provide clues to the shape of the entire skeleton (Fig. 1.5). One of these plates is shown in Fig. 1.6.

As seen from Figs. 1.4, 1.5 and 1.6, *Sprincrinus* has a globular test and five ambulacra that include one single ambulacrum plus two pairs. The mouth of the animal is at the top of the test. One aspect that is not clear from the available fossils of *Sprincrinus* is the position of the anus. The assumption that *Sprincrinus* had a through-going gut seems reasonable.

An intact *Sprincrinus* specimen is a top priority target for field paleontology. If found, it will provide both a test of the reconstruction presented here, and provide

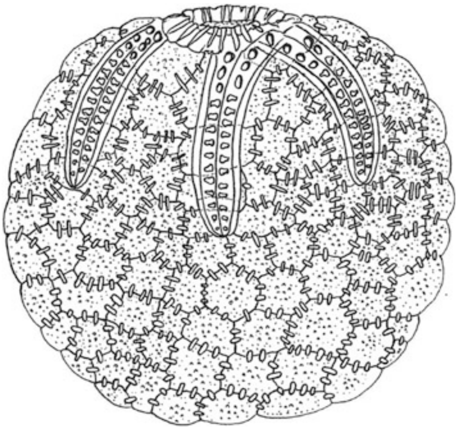

Fig. 1.4 *Sprincrinus inflatus* n. gen. n. sp., the earliest known crown group echinoderm from the Lower Cambrian Poleta Formation, eastern California. Reconstruction of entire skeleton; width of skeleton or test approximately 4 cm

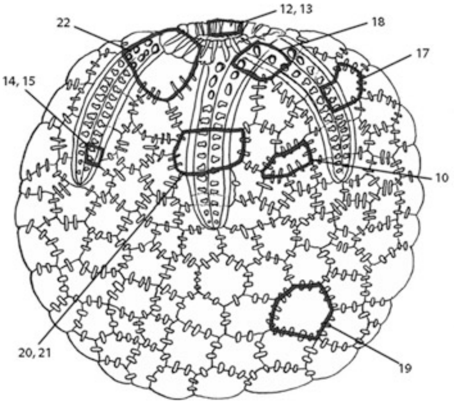

Fig. 1.5 *Sprincrinus inflatus* n. gen n. sp. Sketch map showing positions of various plate types on the reconstructed globular test. Numbers refer to illustration of disarticulated plates as individual figures in Plate 25 of Sprinkle (1973)

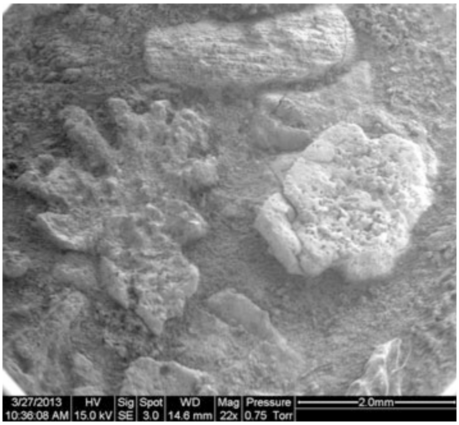

Fig. 1.6 *Sprincrinus inflatus* n. gen n. sp. Associated, disarticulated plates preserved in Cambrian limestone. *Top plate* in the photomicrograph is seen in cross section, showing the stereom microstructure characteristic for crown group echinoderms. Field sample 6 of 6/13/84, Lower Poleta Formation, White-Inyo Mountains, California. Scale bar = 2 mm

further information about the position of the anal plate and other skeletal plates. An essential task is the identification of such specific field research targets. My experience suggests that it is much easier to find the desired fossils in the field if you know what to look for.

Another early group of early echinoderms, the edrioasteroids, first appear in the Middle Cambrian. Suggestions that the Proterozoic Ediacaran fossil *Arkarua* is an edrioasteroid can be discounted, as the similarities are superficial—pentaradial shape has appeared time and again in vastly different organisms due to homoplasy or convergent evolution. Similarly, arguments that the Ediacaran *Tribrachidium* is a triradiate edrioasteroid ancestor are rendered invalid by the discovery of *Gehlingia dibrachida*, a bilaterally symmetric vendobiont that is undoubtedly related to *Tribrachidium* due to the presence of 'thumb structures' (short projections from the trunk ridges; McMenamin 1998) in both *Tribrachidium* and *Gehlingia*.

The edrioasteroid body plan has an interesting feature, namely, the mouth of an edrioasteroid is close to the anus and both occur on the upper surface of the animal. That means that the animal's gut has been deformed into a "U" shape. If we assume that the first echinoderms had a *toroidal body form*, namely, a fat sausage-like sheath enclosing the hollow gut tube (this is thought to reflect the shape of the earliest animal (Jockusch and Dress 2003)), then the edrioasteroid baüplan bends the torus so that both the anus and the mouth are close together on the upper surface of the animal. This makes functional sense, as the mouth must face upwards in order for a sessile suspension-feeding animal to acquire food, and an anus that faces upwards will speed removal of waste by ambient currents.

Let's then imagine the earliest echinoderm as a plated fat toroid with a central tubular gut and five ambulacra radiating from the oral pole (peristome) of the torus. This essentially describes the reconstruction of *Sprincrinus*. For modeling purposes, suppose that the toroid is divided into lines of longitude and latitude to form a rectilinear grid (or morphogenetic field) over the surface of the torus, and then these lines curve around both ends to form a corresponding grid on the inner surface of the tube. If the tubular gut is bent into a "U" shape, the latitudinal field lines are going to be distended and the herniation that results could lead to an outpocketing of the body wall on the side opposite the opening of the U. Indeed, this point opposite the mouth is where stalks or stems often appear in diverse types of echinoderms (*Gogia*, blastoids, crinoids) and echinoderm stem groups (*Cotyledion*). Thus the echinoderm stalk is a herniation in the grid lines or field lines of a distended 'ventral' torus. Intercalated plates in a crinoid stem continue to stack up through ontogeny; in a sense they represent an attempt to "heal over" the herniation breach by intercalation. This becomes a permanent center of sclerite addition and can take on a bulblike structure as a herniation bubble (Boardman et al. 1987):

> A few Paleozoic crinoids have a large bulblike structure at the end of their stem, which either sat on the seafloor to stabilize the crinoid or was filled with gases for flotation. Stems in some primitive crinoids have multipart columnals made up of four to five segments; the earliest reported crinoid from the Middle Cambrian [*Echmatocrinus*] has a primitive holdfast of numerous plates, an elongate extension of the lower calyx used to attach the crinoid to an object on the substrate.

The affinities of *Echmatocrinus brachiatus* are controversial, with some rejecting a crinoid affinity in favor of an octocoral affinity. The presence of what I consider to be stereomic microstructure (its "ridges surface texture" also occurs in the stereom of later echinoderms) on the holotype of *Echmatocrinus brachiatus* (Ausich and Babcock 1998, their Plate 1) suggests that *Echmatocrinus* is indeed an early pelmatozoan echinoderm (Sprinkle and Collins 1995), albeit with eight rather than the usual five arms. Zamora et al. (2013) consider the affinities of *Echmatocrinus* to be unresolved. A holothurian affinity should be considered for *Echmatocrinus* considering the similarity of its arms to simple branched holothurian arms, and the similarity of its conical calyx to the calcareous crown of a sea cucumber, including its polian vesicle (Kondo 1972, pp. 130–131).

The bizarre carpoid echinoderms show another aspect of this distension relationship in their foretails with their wedge-shaped sclerites (plus irregular plates filling in any gaps) in the stele ('tail') as in the Ordovician homoiostelean homalozoan *Iowacystis*. A possible pre-stereom Early Cambrian echinoderm stem group, the vetulocystids (Shu et al. 2002), have a presumably bent gut that ends in plated orifices, with a bulbous 'tail' projecting away from the U-shape gut in what may be another case of distension. This 'toroidal distension equals stem' concept applies to all stalked echinoderms, known collectively as pelmatozoans. Vetulocystids are from the Chengjiang deposit, and thus represent another apparent case of phylogenetic telescoping.

But what of the other side of the torus, where the mouth and anus are brought close together? Here the latitudinal field lines experience such great anterior-posterior compression that one or more of them is liable to split apart like the fabric of a garment parting along a seam. Curiously, the hydropore split as seen in edrioasteroids has this seam-splitting orientation, namely, a lenticular split in the compressed morphogenetic field between mouth and anus. This is geometrically similar to the formation of Lake Baikal, the largest and deepest freshwater lake, by compressive tectonic forces resulting from the collision of Asia and the Indian subcontinent.

The distension described above represents one plausible distortion of the "echinoderm urtorus," but what of bizarre early echinoderms such as spiral *Helicoplacus*? Let's say for the sake of argument that the original centers of mineralization in the echinoderm ectoderm were at the approximate intersections of longitudinal and latitudinal morphogenetic field lines. This patterning would lead to a geometric array of plates covering the outer surface of the animal, somewhat similar to what is seen in *Sprincrinus*. The array of plates (the echinoderm scleritome) would then take on some sort of closest-packing arrangement, leading to, say, rectangular, square or hexagonal plates, or circular plates of different sizes as seen in *Gogia's* stem and the stem of *Cotyledion*. In the latter case especially, the morphogenetic field grid would be divisible into finer gradations between first order field lines. The scleritome is a coat-of-mail like collection of biomineralized elements or sclerites that unite to form an articulating hard skeleton over the surface of an animal; the collective whole of sclerites on the surface of a single animal is called the scleritome.

Table 1.1 Laws of Morphogenetic Evolution

First Law	The same forces that control macroevolution control the observed high precision of convergent evolution. Both processes are associated with transformations of morphogenetic fields (McMenamin 2009)
Second Law	Evidence for developmental control by morphogenetic fields is most apparent in the earliest representatives of any particular lineage of complex life (McMenamin 2009)
Third Law	Higher evolutionary grades of complex life are characterized by simplification of, or standardization of, their respective morphogenetic fields (McMenamin 2015)
Fourth Law	Sexual selection can generate prominent exceptions to the other laws of morphogenetic evolution (McMenamin 2015)
Sbaglio's Law = Fifth Law	Changing the orientation of field vectors controlling the position of surface ornamentation can alter body surface form. Altering these same field vectors can *also* fundamentally alter actual body form (=baüplan)
Sixth Law	Surface-normal field lines occur at the intersections of latitudinal and longitudinal morphogenetic field lines

Recall that each echinoderm plate consists of stereom skeleton, and that the c-axis of each stereomic calcite crystal is generally oriented normal to the surface of the echinoderm test. This observation implies another law of morphogenetic evolution:

> Surface-normal field lines occur at the intersections of latitudinal and longitudinal morphogenetic field lines.

The laws of morphogenetic evolution can be summarized as follows in Table 1.1.

The surface-normal field lines are the field vectors mentioned in our discussion of Sbaglio's Law. They can help determine the points of primordia for nascent mineralization. Sbaglio's Law can help clarify the evolutionary transition from the primordial urtoroidal 2-1-2 ambulacra echinoderms to spiral *Helicoplacus*. As in the formation of a cowlick, the surface-normal field lines are approximated by the c-axes of the stereom crystals that form the echinoderm scleritome. The spines on an echinoid are essentially primary surface-normal field lines that have been reified by a linear projection of stereom. For example, these normal field lines appear very prominently in the early Middle Cambrian early echinoderm *Ctenoimbricata spinosa* from southern Europe.

The surface-normal field lines of *Sprincrinus* are perpendicular to the surface of its globular test. In *Helicoplacus* and other spiral echinoderms, the surface-normal field lines have been offset or tilted in an imbricate cowlick fashion, imparting a spiral to the entire stereom skeleton. As a test of this inference, we must seek spines or other indicators on the outer surface of the spiral echinoderm as a test of whether or not they follow this inferred pattern of morphogenetic field line distortions. The spiral echinoderm *Helicocystis* shows just this pattern, with short spines actually visible on its test, inclined about fifty degrees from vertical (or normal to the test surface), and inclined in the direction of the mouth at the top of the animal (Smith and Zamora 2013). This is precisely the prediction of morphogenetic field analysis.

To proceed further with this analysis, and to lay bare its more general nature in the sense of the "common latent morphogenetic potentialities" (Vorobyeva 2003), we must consider the nature of the hourglass on the abdomen of a black widow spider. The pigmentation pattern on venomous spiders of the genus *Latrodectus* includes the deadly North American black widow spider. Several species have been assigned to this genus; they are all popularly called black widows. These spiders are known for painful, sometimes fatal bites from females, their sexual cannibalism (hence 'widow'), and for the unusual hourglass pattern, usually in garish red, on the underside of the typically black abdomen. An odd type of cannibalism occurs in the Black Lace-Weaver Spider (*Amaurobius ferox*), where juveniles feed first on the unhatched eggs of their siblings and next, in a case of matrophagy, on their own mother, who actively encourages the cannibal feast.

Does the hourglass marking provide any clues about spider morphogenesis? If we consider *Latrodectus* in its Old World representatives, particularly the Mediterranean Black Widow *L. tredecemguttatus*, we observe a pigmentation pattern that is more complete and complex than that seen in North American *Latrodectus*. The species name of the Mediterranean Black Widow refers to the thirteen spots visible on the upper abdomen of the species in both males and females. Figure 1.7 shows the pigmentation on the upper surface of the abdomen of a female of *L. tredecemguttatus*. It is important for our analysis to elucidate the relationship between the thirteen-dot pattern of *L. tredecemguttatus* and the hourglass pattern of North American species of *Latrodectus*.

Note that in Fig. 1.7 that there are only actually ten spots, because the lower three spots have fused with spots eight, nine and ten to form rough figure eight patterns. This is analogous to the fusion of Cambrian sclerites (Landing 1984) as known to occur in *Lapworthella*. Clearly, the hourglass shape, on the underside of

Fig. 1.7 Pigmentation pattern on the upper surface of the abdomen of a female of the European *Black* Widow (*Latrodectus tredecemguttatus*), Croatia. Photo credit: K. Korlevic

the abdomen, can be thought of a analogous to two once separated spots that have fused as in the case of spots 8–13 in *L. tredecemguttatus*. These are the spot pairs close to the posterior tip of the abdomen, where another spot is faintly visible.

In a reduction-of-spots effect that recalls Williston's Law (the law of evolutionary reduction-of-parts), an original spot pattern of more than thirteen spots in the ancestor of modern *Latrodectus* has apparently been reduced to only two spots (the lone hourglass) in North American species. It is thus a fundamentally different process than, say the orientation of stripes in a Turing pattern, determined as they are by production gradient, parameter gradient and diffusion mechanisms (Hiscock and Megason 2015).Whether the full spot pattern is an atavistic reflection of the pattern of sclerite primordia covering a Cambrian stem group form is unknown, but a thought worthy of further exploration.

As seen in Fig. 1.7, the spots in *L. tredecemguttatus* dorsal abdomen may be numbered 1–13. Note that the spots are aligned into three anterior-posterior rows, with the central row spots larger and rounder, and the lateral spots more elongate and in some cases drawn out into teardrop shapes that somewhat resemble the lateral spines in the Cambrian halkieriid *Halkieria evangelista*, or resemble even more closely (Donovan et al. 1994) the Lower Ordovician *Dimorphoconus granulatus*. Indeed, we may use this spot pattern as a proxy to explain the scleritome origins of many modern animal skeletons. A system-wide field rather than, say, diffusion of morphogens, morphogen gradients, etc. may control this morphogenetic patterning.

The morphogen concept is elegant and useful for explaining divaricate shell patterns (Seilacher 1972), but it is too reductionist for some problems of morphogenesis, such as: How can body plan change rapidly? The morphogen concept will be of little use by itself to explain the phylum grade rapid evolutionary change that we see in the Cambrian Explosion. Any solution will require modification of a torus controlled by a morphogenetic field that can change (or be induced to change) rapidly, at a pace much faster than allowed by conventional Darwinian evolution by means of gradual natural selection (also known as microevolution).

Bob Hazen has argued that patterns develop "simply through local chemical signaling or diffusion-controlled reaction process," implying that it was unnecessary to "to bring toroids into such surface patterning." It is true that certain diffusion systems can "generate regularly spaced spots or stripes of morphogen concentration" such as Turing patterns that can, in turn, "induce primordia of skeletal elements" (Newman and Bhat 2008). This represents an important critique of the system-wide, morphogenetic torus field approach.

The critique, however, founders when confronted with evidence from the fossil record. Diffusion processes alone, important as they may be for the generation of gradient patterns such as those of divaricate shells, are insufficient to account for the nature of the metazoan scleritome. This can only be explained by reference to a morphogenetic field as tied to an elongate- or elliptical-toroidal metazoan body plan. Fossils provide evidence for the critical importance of this toroidal field, and the results may be quantified.

Consider a toroidal membrane with both latitudinal and longitudinal lines on both the inner and outer surfaces of the toroidal membrane. Let's refer to the openings at either end of the toroid as the poles. As on a conventional globe of the Earth, the lines of longitude converge at the poles; the spacing between the lines of longitude gets smaller and smaller as you go north or south, and vanishes to zero at the pole itself.

This geometrical pattern is key for understanding the scleritome from the perspective of morphogenetic torus theory. Paleontologists developed scleritome analysis in the 1980s as method of explaining the "small shelly fossils" that were turning up in impressive numbers in the Lower Cambrian limestone acid residues. These residues were being searched for clues to the origin of animal phyla (Landing 1984). Mineralized sclerites of the small shelly fossil type first appear in the earliest Cambrian or latest Proterozoic. Sclerite-like forms have been reported from somewhat earlier strata, but they are preserved as organic material and are not mineralized or at least not very heavily mineralized (Moczydlowska et al. 2015).

In May 1986 I attended a geological workshop in Uppsala, Sweden, entitled "Taxonomy and Biostratigraphy of the Earliest Skeletal Fossils." The purpose of the workshop was, among other things, to advance our paleontological knowledge about the tiny fossils from the Cambrian acid residues. These curious and beautiful little fossils were attracting a lot of geological attention at the time, as they promised important insights into the Cambrian Explosion problem. Most of these fossils are shells or shell fragments about a millimeter or less in length, resulting in their nickname "the small shelly fossils" (Matthews and Missarzhevsky 1975).

I shared at the meeting a fossil from my field research in México. To my delight at the time, it generated a certain amount interest among the other scientists. It was a specimen of the small shelly fossil *Microdictyon*. The fossil, only a millimeter or so across, looks under magnification (Fig. 1.8) like a porous bit of fine lacework, with a partly rounded outline and with the pores organized into a geometric pattern.

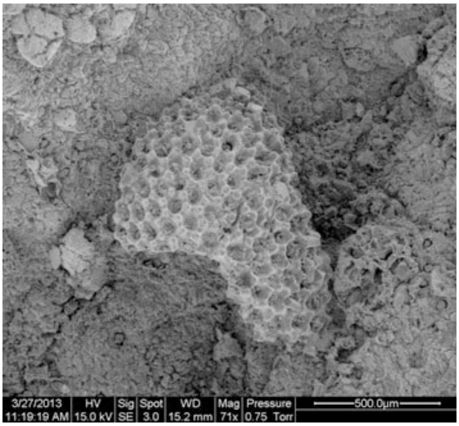

Fig. 1.8 *Microdictyon multicavus*. SEM photomicrograph of a small shelly fossil specimen naturally exposed on the surface of a limestone, Puerto Blanco Formation, unit 2, sample 5.5 of 12/17/82, IGM 3645, scale bar = 500 µ

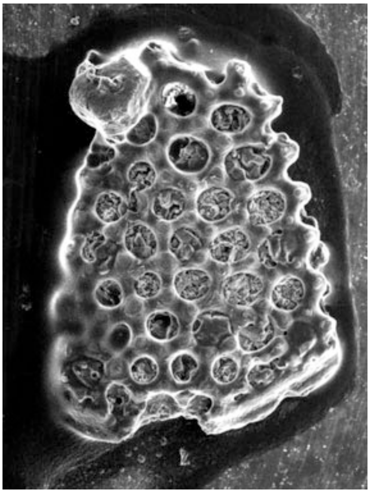

Fig. 1.9 *Microdictyon multicavus*. From acid maceration residue small shelly fossil from Unit 3 of the Puerto Blanco Formation, northwestern Sonora, México, field sample MM-82-49. Maximum height of specimen 0.7 mm

Most small shelly fossils such as *Microdictyon* are recovered from rock by being dissolved out of limestone with acid in a process known as acid maceration (Fig. 1.9). But the mere recovery of the fossils did not help us to understand very much about the biology of *Microdictyon*. The problem was solved a few years later by Chinese paleontologists, who discovered complete specimens of the *Microdictyon* animal (Chen et al. 1989; Bengtson 1991). Evidently many of the small shelly fossils were tiny bits of mail-like skeletons, formed of skeletal elements called sclerites. The sclerites aligned in rows along the side of *Microdictyon* are called trunk plates.

The morphology of *Microdictyon* is unusual because its trunk plates are isolated from one another on the dorsal surface of the animal. If this represents a reduced version of a formerly more extensive scleritome, then we have an example of Williston's Law. The case of *Microdictyon* would then be comparable to the reduction of the spider color pigmentation pattern to a relict hourglass shape. This is not necessarily the case, however; in the *Microdictyon* lineage the porous sclerites along its back may always have been isolated points of skeletonization. Interestingly, there is evidence for molting in *Microdictyon*, as specimens have been found in which the base of a small sclerite was attached to a larger sclerite, presumably due to incomplete separation of the preceding molt (Caron et al. 2013).

Intact scleritomes are only rarely seen as fossils. When they are discovered, they prove to be extremely important for determining the biological affinities of the scleritome bearer. Perhaps the best example of an intact scleritome comes from Lower Cambrian rocks of the Sirius Passet region of Greenland. The fossil is called *Halkieria evangelista*, an amazing find that gives us otherwise unavailable information about the morphology of the spiny halkieriids (Conway Morris and Peel 1995).

Halkieria evangelista is a worm- or slug-like creature a few centimeters in length. If it were naked it would probably resemble an elongate nudibranch or sea slug. The upper surface of *Halkieria evangelista* is covered in several types of pointed sclerites from snout to tail. Palmate sclerites run down the dorsal midline. Two rows of cultrate sclerites run on either side of the palmate sclerites, defining lateral rows. At the outer edge of the metazoan is a belt or girdle of siculate sclerites. This belt runs all the way around the edge of *Halkieria* except at the tip of the anterior end of the animal, where the siculate sclerite belt vanishes.

Before discovery of the intact *Halkieria* scleritome, its fossils had been studied as disarticulated pieces recovered by acid maceration. The small shelly fossils did not prove particularly helpful for reconstructing the complete body form. But with the fossilized scleritome now in hand, it becomes possible to unite all the *Halkieria* sclerites into a unified scleritome. The complete specimen offered some big surprises. Both the head and tail end of the animal hosted very large sclerites that each strongly resembled the disarticulated shells of a brachiopod. The two large sclerites are connected by the dorsal rows of smaller, palmate sclerites.

If the large sclerites of *Halkieria* had been found in isolation, as solitary fossils as could happen when paleontologists pick through acid maceration residues to find small shelly fossils, the large sclerites likely would have been mistaken for individual brachiopod valves. Several researchers have argued that brachiopods are descended from halkieriids, and that the brachiopod body form is in fact a foreshortened halkieriid (Conway Morris 1998) that has lost its midriff small shelly sclerites and is down to only two, the dorsal valve and the ventral valve. This of course requires a bend in the body torus and gut that is comparable to the echinoderm case. Other scenarios for brachiopod origin, involving a stalk-bearing tubular form with many sclerites (Skovsted et al. 2011), also require a bend in the torus as seen in a phoronid (a member of a worm-like phylum related to brachiopods because of its crown-of-tentacles or lophophore).

We must now ask: Why did halkieriids grow relatively broad, flat valve-like sclerites on either end of their scleritome? Surely the halkieriids were not consciously anticipating some future bivalve form. It was once seriously argued that the anterior and posterior protovalves were used to block off the front and back ends of a U-shaped burrow. I think this is pretty unlikely, however, because the burrow would have to be actively adjusted to maintain exactly the right length. Otherwise the protovalves would not be much use as manhole covers.

The answer must involve the morphogenetic field of the torus. Recall that the lines of longitude converge as you approach the poles. For a particular species, there may be some critical density of field lines that triggers a transition from an individual, relatively large sclerite (formed in its own, roughly square box of longitude and latitude, with or without a spinous projection on the ‘Z-axis’ [= C-axis for echinoderm surface plates] normal to the body surface) to tiny and perhaps fused sclerites (where the boxes pass some threshold of rectangular, poleward elongation). The fused sclerites could then merge to form the broad, flat valve-like sclerites of a halkieriid. Note that a morphogen diffusion explanation does an inadequate job of explaining the anterior miniaturization of sclerites (sometimes occurring in a long series, as in the radula) unless the morphogens themselves are channeled along some sort of converging ultrastructural conduits.

The halkieriid animal is programmed to form sclerites only on its upper surface. If this were not the case, we would expect four protovalves to form, one dorsal and one ventral on each end of the animal. The toroidal field lines controlling skeletal morphology can evidently be switched "off" and inhibited from producing sclerite primordia on the underside of the animal. This was apparently the case for *Halkieria*, considering that it only has sclerite armor on its upper half (a few siculate sclerites do occupy a marginal-ventral position). The fact that the morphogenetic grid can have fields or zones edited to eliminate sclerite production has far-reaching implications.

A Siberian small shelly fossil known as *Maikhanella* demonstrates the scleritome field genesis of protovalves. *Maikhanella* is a protovalve small shelly fossil from a halkieriid-like Cambrian creature whose articulated scleritome remains unknown (Bengtson 1992). Isolated sclerites of *Maikhanella* occur in Sichuan, China (Steiner et al. 2004). However, the protovalve of this animal is important, because it is clearly composed of tiny, partially fused sclerites. Sponge spicules form by fusion of smaller, simpler sponge spicules (McMenamin 2008). But with *Maikhanella*, we see sclerite fusion under local control of a morphogenetic field.

If we get closer to the toroidal pole, we see the lines of longitude converge. We would thus expect the sclerites to get smaller and smaller, approaching the vanishing point, and this is indeed what we observe. Mollusks such as snails and chitons feed by means of the molluscan radula. Undoubted radulas date back to the Cambrian (Butterfield 2008). The process of miniaturization of a scleritome to form radula-like mouthparts (Zhang et al. 2015a, b) is quite evident in the Early Cambrian Chengjiang specimens of *Wiwaxia papilio*. In a theme that we will hear repeated many times in this book, the record of wiwaxiids in Cambrian stages 3–5 reveals "morphological stasis in the wake of the Cambrian explosion" (Yang et al. 2014). Yang et al. (2014) argue, correctly in my view, that the ancestral mollusk was a scleritome-bearing organism because this "would account for the presence of microvillar 'chaetae'" in early conchiferans such as the snail-like small shelly fossils *Aldanella* and *Pelagiella*.

The radula is shaped like a sanding belt and has a motion like that of an escalator. Each radula is covered with tiny teeth, composed of magnetite. These tooth rows are used by the animal to grind away at the surface or matrix (often porous rock) hosting its microbial food. Snails and chitons use their radulas to grind away at rock and eat the algae and bacteria that live in the porous rock surface. Mushroom-shaped islands are formed in shoreline limestone, carved into improbable notched cliffs by this grinding action (Lowenstam 1974). These islands eventually topple over when the narrow neck of the mushroom island breaks through. Radulas are thus responsible for sculpting the unique geomorphology of these mushroom islands.

Cephalopods (squid, octopus, nautiloids, ammonoids) have radulas as well, and these are usually combined with a biting parrot-like beak. Squids and ammonoids have seven radular teeth in each transverse row of radular sclerites, whereas in *Nautilus* there are nine teeth in each transverse row (Nixon 1996). The cephalopod family Bolitaenidae, as well as *Nautilus* and the octopus, have radular teeth that look very much like the teeth or elements of conodonts, an extinct family of marine early chordates that utilized dentine in their sclerites and are now usually classified as vertebrates (Briggs et al. 1983).

The anterior collection of sclerites in a conodont is called the conodont apparatus, and it is the vertebrate counterpart to the molluscan radula. Indeed, the medial S_0 element (also known as the trichonodelliform element) of the conodont apparatus greatly resembles the large, medial rhachidian tooth of the cephalopod radula. Both conodont elements (S_2–S_4 elements) and cephalopod radular teeth (L_1 and L_2 lateral teeth) also have a pectinate (comb-like) aspect, greatly increasing the overall resemblance. An analogous shredding function for both scleritome types is implied. In a harmony of scleritomal embouchure, both the pectinate conodont elements and pectinate radular teeth respond to first order and second order field lines in the comparable arrangements of regularly spaced primary and subsidiary sub-teeth on the conodont elements and radular teeth, respectively. A second order field is also evident in the rhomboid, cancellate patterns (Caron et al. 2013) seen on the spines of the lobopodians *Hallucigenia* and the comparable small shelly fossil *Rhombocorniculum*.

The radula and the conodont apparatus, however, are neither strictly homologous (like the flippers of a dolphin and an ichthyosaur, structures sharing common origin from a limb in a shared ancestor) nor analogous (like the wings of a fly and a bat, similar features evolved from different structures by convergent evolution). Functional analogy (either by evolution from homologous or non-homologous structures) is the usual mode proposed for convergent evolution.

We need a new term to describe this relationship between radular tooth arrangement and the conodont apparatus. These features result from a similar morphological manifestation due to a shared common pattern: the toroidal metazoan morphogenetic field. This shall henceforth be referred to as an evolutionarily *torologous* relationship. Torologous features are widespread, and include the pectinate conodont elements S_2–S_4 elements and the pectinate cephalopod radular L_1 and L_2 lateral teeth.

The fundamental phenomenon is caused by the roughly orthogonal morphogenetic field lines converging in the oral region. In vertebrate zahnreihen, tooth rows and even cusps within individual teeth respond to field lines that sometimes run at a curious angle across the upper surface of the jaw. This relationship has puzzled vertebrate paleontologists for many years. The problem was finally resolved with description of the new tetrapod Class Paramphibia (McMenamin 2015).

Torologous structures form via convergent evolution directed by response of the generation of skeletal primordia, etc., to the concentration of field lines at the, say, anterior end of the toroidal morphogenetic field as seen in the molluscan radula and conodont apparatus. This concept of torologous evolutionary features will greatly facilitate our approach to understanding parallel evolution, iterative evolution and recurrent evolution. Convergent evolution in all these cases is the result of a response to a torologous substrate of morphogenetic field lines.

The general “ur-toroidal” pattern is highly conserved between phyla; indeed, kingdoms other than Animalia likely share it. However (there is considerable irony here), the network pattern and editorial adjustments to the morphogenetic grid can happen suddenly and lead to near instantaneous major morphological change. This can be rendered as heterochrony-style morphological change without any requirement to change ontogenetic-developmental timing. The change can be sudden and heritable. I will demonstrate below that morphogenetic grid adjustment is a fundamental driving force for evolutionary and developmental change.

Explanations of recurrent evolution that rely on regulatory genes to “function as morphogenetic switches” (Gompel and Prud’homme 2009) are doomed to failure because they cannot explain the overall function of the morphogenetic system. Such genes may play subsidiary roles in editorial changes to the grid, but even this is not certain. To enact major morphological change, the influence of many genes would seem to be required, and this thereby acquires the problem of having to *coordinate* all the gene morphogenetic switches to accomplish the major morphological change. This is the problem of “directed mass mutation” articulated by Berg (1969). The impossibility of making changes via conventional natural selection to the refractory kernels of the gene regulatory networks is apparently insurmountable especially when the changes are major and rapid as during the Cambrian Explosion (Erwin and Valentine 2013).

Rapid major change especially requires system control, and the torus morphogenetic field is a scientifically plausible part of the control that can direct the system. The Cambrian Explosion, and its attendant appearance of many new phyla, must have an inherently torologous aspect. Field lines are potentially reoriented *en mass* in a single event or events, thereby allowing for very rapid and significant morphological change.

The implication here of course is that the field lines *lead*, and the genome *follows*. The central dogma of biology, which purports to explain the “flow of genetic information in a biological system” (as the current Wikipedia entry entitled *Central dogma of molecular biology* puts it), has just been completely reversed if the conjectures outlined here are confirmed. An alternate perspective would argue that the field lines and genome were altered simultaneously by some external agency.

Suggesting an inversion of the central dogma is a bold claim. Can this actually be the case? According to Jonathan Edwards (personal communication, January 12, 2016), to “influence DNA in an ‘intelligent’ way would require a machinery that has never been found and which would have to take up a large amount of space in the organism if it did. It is totally implausible as far as I can see. An there seems to be no need for such excess.” Is it possible that the morphogenetic field associated with the surface of metazoa provides just such machinery? I disagreed with Edwards, and said in reply:

> There does indeed appear to be a need for something beyond ordinary changes to nuclear DNA (in accordance with the Central Dogma) to explain alterations to the kernels in developmental gene regulatory networks (GRNs), especially when change is rapid as during the Cambrian Explosion. The conventional neo-Darwinian perspective is failing here on scientific terms.

There does appear to be a need for overarching system control. But what could that possibly be? Instead of taking up space inside of the organism, an elegant solution might appeal to the grid pattern that is associated with the *surface* of an organism.

The radula is a miniature scleritome, formed by the tight convergence of latitudinal field lines near the anterior pole. The sclerites do not fuse in this case, but rather retain their separate identity in order to function as the teeth of the grinding radula. Interestingly, radular teeth are so common as disarticulated bits in the sediment that they are able to impart a magnetic signature to sedimentary rocks, and are thus quite useful for paleomagnetic studies. After the mollusk dies and the radula's soft tissue decays, the disarticulated magnetite radular teeth orient themselves as tiny magnets in sea floor sediments.

The Cambro-Ordovician chiton *Matthevia* is another paleontological demonstration of the toroidal scleritome, again emphasizing the essential value of paleontology to biology, as fossils elucidate the possibilities of pattern and form that are no longer visible in the living world. Most reconstructions of *Matthevia* show the spiny sclerites along its back (similar to the position of the palmate sclerites in *Halkieria*) with the largest at the dorsal center of the animal, and the sclerites decreasing in size in both the anterior and posterior directions as the field lines converge. This is in accord with the fact that the morphogenetic torus field rectangles (that is, intersection of "first order" latitudinal and longitudinal field lines to form rectangles) are largest right along the equator of the torus where the separation or distension of the field lines is ordinarily the greatest. The Stinchcomb and Darrough (1995) reconstruction of *Matthevia* shows the sclerites becoming relatively narrower, in accordance with the elongation of the field boxes (delineated by roughly orthogonal field lines) as one approaches either pole, that is, as the longitudinal first order field lines compress rapidly as the pole is approached. This pole-ward stretch is shown well by the problematic Ediacaran fossil *Ausia fenestrata*, which has geometric dimples (instead of sclerites), and these stretch and narrow considerably near the preserved pole of the creature. Indeed, comparisons have been made between *Ausia* and the halkieriids (Dzik 2011). Comparisons of *Ausia* and *Burykhia* to the tunicates are implausible (Fedonkin et al. 2012).

Of course, there is much room here for genetic manipulation of sclerite shape and arrangement in any particular organism. Sclerites in many types of chitons, for example, also decrease in size as one approaches the lateral margin of its scleritome. It seems clear, however, that the torus morphogenetic field primarily controls sclerite placement and size, and adjustments to field lines may also control the sizes of lateral margin sclerites.

The mickwitziid brachiopods (McMenamin 1992; Holmer et al. 2002) are an Early Cambrian group that seems to be descended from halkieriid-like metazoans with many sclerites. The original scleritome was geometrically arranged over the body of the animal, comparable to what we see today in spiny aplacophoran mollusks. The pattern also occurs in the problematic gastrotrich metazoans. Some early brachiopods, and I would include at least some of the stem group mickwitziids in this list, were unable to completely close their shells because the two shells had very different shapes. More evolutionarily derived, bivalved, descendant brachiopods were able to utilize their toroidal field to match their anterior and posterior valves.

The largest known trilobites (700 cm in length; Rudkin et al. 2003) belong to the Ordovician genus *Isotelus rex* (the name puns on *Tyrannosaurus rex*), a trilobite that rather strongly resembles stage four of five in the trilobite ontogenetic-phylogenetic series (Pivar 2009). It might be argued that, on the contrary, *Isotelus,* with its relatively small number of pleural (thoracic) segments is in fact derived from earlier Cambrian trilobites that had more and in some cases many more pleurae. This is in fact the case, and the loss of segments in *Isotelus* would be seen as part and parcel of the reduction of parts seen in many arthropod lineages (Williston's Law), often resulting from either outright loss, or by fusion of once independent segments by tagmosis (Hughes 2003). Malacostracan crustaceans and insects apparently underwent tagmosis or tagmatization independently, in a striking case of convergent evolution in accord with Williston's Law (Abshanov and Kaufman 2000).

Here, however, we begin to see the inadequacies of a conventional evolutionism that focuses too intently on the process of natural selection and consequent pan-selectionist evolutionary pressures. Note how, in the isotelid trilobites, the cephalon (head) and pygidium (tail shield) are precisely the same shape (Fig. 1.10).

There might very well be an adaptive explanation for the cephalon-pygidium matchup. Trilobites were subjected to a new and vicious form of selection during the Ordovician due to predatory attack by emerging voracious cephalopods (such as

Fig. 1.10 Ordovician trilobite *Isotelus maximus* from the Eden Group (formerly Latonia Formation), Cincinnati, Ohio. Some specimens of this *Isotelus*, the state fossil of Ohio, exceed 60 cm in length. The Eden group consists primarily of blue shale beds separated by limey partings. Scale bar in cm

Cameroceras; Teichert and Kummel 1960) with a taste for trilobites. These Ordovician nautiloids, some of which grew shells reaching an astonishing 5 meters in length, forced trilobites to enhance their protective morphologies and behaviors. A stalwart trilobite defensive strategy was to roll up like a pill bug or sow bug. This particular behavior was rare before the Cambrian but quite common beginning in the Ordovician.

Naturally, the roll-up defense is more effective if, once enrolled, the edge of the carapace can make a perfectly smooth seal. Hence the exact match between the cephalon and pygidium in *Isotelus* has considerable defense value. But rather than being a step by step process of slow selection favoring trilobites with increasingly tighter fit between heads and tails (the classic selectionist story of evolutionary optimization), the problem was likely solved for *Isotelus* in a single evolutionary step. In a torus-related development, the carapace of early isotelids changed to conform more closely to the ur-toroidal shape. The cephalon and pygidium were thus quickly rendered a nearly exact fit, because symmetrical ends of the morphogenetic torus molded the shape of both.

This is an important point, for it impinges directly on our understanding of the evolutionary process. For natural selection to operate in the conventional understanding, there has to be a more or less randomly generated series of overbite trilobites that don't match up very well when they attempt enrollment. Cephalopods easily subdued the mismatched misfits by prying open the trilobite carapace at the zone of cephalon-pygidium edge separation. The few lucky trilobites with better fit were harder to eat because their smoother rolled surface protected their entire soft underside; hence they survived and left more prodigies, or rather, progeny.

This is a fallacious "just so" story, and may be rightly subjected to criticism. It puts the selective carriage before the morphogenetic horse. Natural selection has a role to play, to be sure, but its role is editing out toroid mismatches after the toroidal cephalic-pygidial fit is already more or less established. And herein lies the great strength of biological structuralism. Genes exist, yes, natural selection could conceivably occur after the fact, yes, but the change of interest is actually a response to constraints of a toroidal membrane, and that is what really generates animal shape.

Ryan (2003) demonstrated that the Ordovician brachiopod *Apheorthis lineocosta* was probably unable to close its shells because of a serious valve mismatch. Thus it represented an evolutionary holdover from the Cambrian, a stem-group brachiopod comparable to mickwitziids that never acquired the ability to close up its shell in a bivalve fashion. In an analogy with *Isotelus*, neither many mickwitziids nor *Apheorthis lineocosta* made the dorsal anterior-posterior torologous match that would have allowed them to attain the evolutionary grade of proper bivalve.

We may mathematically model the scleritome morphogenetic field by plotting the following equation:

$$f(x) = \mathrm{sqrt}(5 - (\mathrm{abs}(x)^\wedge 1.05)) \tag{1.1}$$

In other words, the function f(x) is equal to the square root of five minus the absolute value of x raised to the 1.05 power. This will produce a curve that simulates the dorsal profile of a slug-shaped scleritome-bearing Cambrian animal such as a halkieriid.

We can use this plot to identify regions of the field where sclerite fusion or miniaturization are most likely. Individual sclerite width will be at a maximum when the derivative of the function f(x) is set to zero, in other words, right at the center of the plot in Fig. 1.11. For the purposes of calculation we will introduce two parameters, a and b. Let's set a to have a value of 3, and b to have a value of 4. We will set the c value as follows: the f(x) curve intersects the x axis at c and *negative c*. Values of the function from $0 < |\mathrm{x}| < \mathrm{a}$ will show large individual sclerites along the back of the animal as in *Matthevia*, with sclerite maximum size decreasing in concert with the graph in Fig. 1.11 in two directions. Values from $a < |\mathrm{x}| < b$ constitute the 'protovalve' zone, where (as in *Halkieria*) clusters of small (but not too small) sclerites are prone to fuse at nodes.

Values from $b < |\mathrm{x}| < c$, with

$$f(|c|) = 0 \tag{1.2}$$

will tend towards either sclerite loss or sclerite miniaturization; this could be called the radula zone or the conodont apparatus zone, or even the *torologous zone* due to its propensity to be associated with cases of torologous convergent evolution (Stokstad 2003).

In certain organisms the polarity of sclerite size within each zone can be reversed, namely $0 < \mathrm{x} < a$, $a < \mathrm{x} < b$, $b < \mathrm{x} < c$, as in the case for sharks and other elasmobranchs that have tiny sclerites at the torus equator (sharkskin) and larger ones at the anterior pole (rows of shark teeth). Note that teeth can also evolve

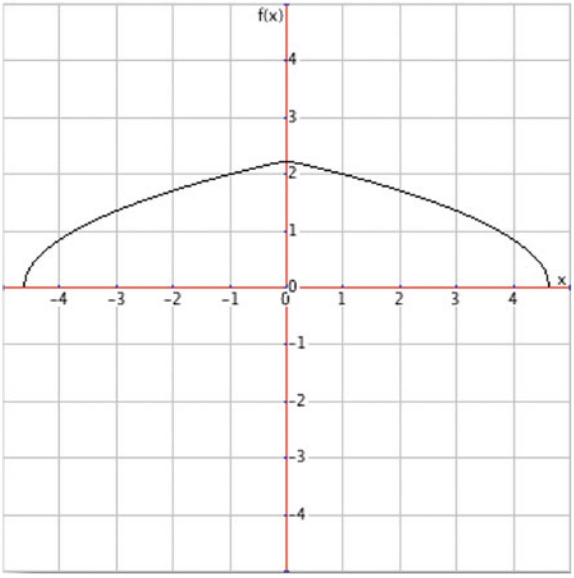

Fig. 1.11 Graph of the scleritome function f (x) = sqrt(5-(abs(x)^1.05)). This curve models the dorsal profile of a scleritome-bearing animal. Individual sclerites would project *above* the *top* surface of the *curve*

(or re-evolve) independently, as for instance in the extinct placoderm fish, in yet another case of convergent evolution (Smith and Johanson 2003). These neo-teeth nevertheless remain under the influence of toroidal morphogenesis, as multiple or set-back rows or arrays of neo-teeth are also known to appear in these fish.

Some extinct sharks such as *Stethacanthus* from the Late Devonian (Maisey 1996) have medium size sclerites in bizarre head projections in the $a <$ x$<b$ zone. The same is seen in the stethacanthid shark *Damocles serratus*, named for the sword that hung precariously over the head of Damocles in ancient Greek legend. The Late Jurassic rabbitfish (chimaeroid) *Ischyodus* shows similar development in its curious "head clasper," a cartilaginous projection capped by sharp sclerites. The comparison between these two suggests yet another case of torologous evolution.

Morphogenetic field lines are generally straight or gently curved over the surface of the torus, but there exists a bizarre exception to this general rule—the new tetrapod class Paramphibia. In *Permodiadonta oklahomae* (nom. corr. herein, ex *P. oklahoma* McMenamin 2015), the longitudinal field lines are compressed to form sinusoidal field lines running from the anterior to the posterior of the animal, as indicated by the animal's unique dentition. Zahnreihe (plural: zahnreihen) are the morphogenetic field lines in the vertebrate jaw region, typically expressed as rows of teeth that may be inclined to the edge of the jaw. The sinusoidal field lines of *Permodiadonta* falsify the hypothesis of control by morphogen concentration gradients (McMenamin 2015):

> Insurmountable difficulties will attend any attempt to explain the diverging and converging zahnreihen in *Permodiadonta* by means of, say, diffusing morphogen compounds. Any such morphogen concentration gradients would have to be so complexly structured that they would resemble, well, a morphogenetic field.

The morphogenetic model presented here predicts that there should be a ring of scleritized tissue in the $a < |x| < b$ or $a > |x| > b$ protovalve zones. This pattern holds for the armadillo (clade Xenarthra, which includes the extinct glyptodonts; Hill 2006; Vickryous and Hall 2006), where the toroidal articulated sphere is armored by fused intermediate sclerite primordia to form the shoulder and tail scute shields. The armadillo seems to aspire to become a "land bivalve", and has arrived at a degree of "bivalved-ness" comparable to that of the stem group mickwitziid brachiopods and *Apheorthis lineocosta*.

Let's return for a moment to the *Microdictyon* sclerites seen in Figs. 1.8 and 1.9. These sclerites are now known to occur in two rows along the flanks of the lobopod (catepillar-like) marine animal. We can think of this as a latitudinal row of sclerite primordia, with the anterior tip of the torus serving as the protovalve zone, unmineralized in this case. This is likely to be a genetic and/or morphogenetic field-controlled departure from the $a < |x| < b$ or $a > |x| > b$ protovalve zone general rule. But it nevertheless seems reasonable to infer that the somewhat valve-like sclerites of *Microdictyon* are built up of fused sclerites, as is the case for *Maikhanella*.

Note the seemingly geometric arrangement of the presumed fused sclerites in Figs. 1.8 and 1.9. It is as if the sclerite itself has preserved the orthogonal array of morphogenetic field lines that characterize the animalian, toroidal dorsal ectoderm.

Fig. 1.12 *Dimorphoconus granulatus*. Reconstruction of the scleritome of this Ordovician benthic marine animal. Modified from Donovan et al. (1994). Scale bar = 1 mm

In other words, the *Microdictyon* sclerite is a mineralized patch of morphogenetic field, a paleontological equivalent to the hourglass logo of the black widow spider. Compare the scleritome of the Early Ordovician marine scleritome-bearer *Dimorphoconus granulatus* (Fig. 1.12) and note the curious analogy between the positions of the larger sclerites and the pattern on the back of *Latrodectus tredecimguttatus* (Fig. 1.7). We see this same similarity in the newly described spiny Early Cambrian lobopodian *Collinisium ciliosum*. The most prominent sclerites in *Collinisium* are huge spines that project along its dorsal, sagittal midline (Yanga et al. 2015), comparable to the spots along the midline plane of symmetry in *Latrodectus*. This is a clear demonstration of yet another torologous effect.

As expected, anterior and posterior porous sclerites in *Microdictyon* are smaller than sclerites near its dorsal center. The patch of morphogenetic field shows dilatory swelling in the second order and third order field lines, for in a typical *Microdictyon* sclerite the constituent fused sclerite elements are small near the margin of sclerite and larger at its center. This pattern recalls the rosette osteoderms in the glyptodontid armored mammals *Propalaehoplophorus* and *Glyptodon*. The spiked tail club in the glyptodontid *Doedicurus* is torologous to similar features in giant horned turtles belonging to the genus *Meiolania* of Australia and New Caledonia. Both glyptodontids and meiolanid turtles are thought to have been driven to extinction by human predation pressure (White et al. 2010).

Sclerite placement, however, seems to be under the control of the first order field lines. The pinch-and-swell body form of the lobopodian *Microdictyon*, plus the larger sizes of the pores in the center of each sclerite, may suggest a sinusoidal curvature to the longitudinal morphogenetic field lines as has been hypothesized for *Permodiadonta* (Fig. 1.13).

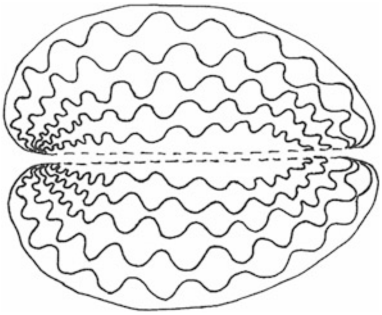

Fig. 1.13 Sinusoidal longitudinal morphogenetic field lines in the paramphibian tetrapod *Permodiadonta*

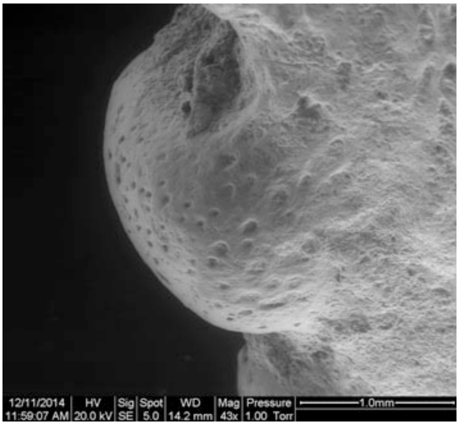

Fig. 1.14 *Permodiadonta oklahomae* McMenamin 2015. Holotype, NCSM 28323. Scanning electron microscopy image of tooth, note punctate tooth surface with punctal tubes penetrating the enameloid surface layer aligned roughly parallel even along the edges of the tooth. Scale bar = 1 mm

Interestingly, subsidiary (second or subsidiary order) field lines are expressed in the *Permodiadonta* enameloid on the upper surfaces of its teeth. Figure 1.14 shows the punctate surface of the *Permodiadonta* tooth. Note how the punctae are strictly normal to the contour of the torus as it bends into the oral cavity, leading the dimples to become elongate/ellipsoidal along the edges of the domal teeth. We are dealing here with the corollary to Sbaglio's Law, namely, the sixth law of morphogenetic evolution that states that the default orientation of field vectors is normal to the surface of the torus. The surface normal field vectors are thus not inclined in this case; rather, the anterior to posterior field lines have been compressed and folded as shown in Fig. 1.13. From the description (McMenamin 2015) of *Permodiadonta oklahomae*:

> It may be possible to fruitfully speculate on how the Paramphibian morphogenetic field acquired its peculiar configuration. Could the wavy longitudinal field lines be the result of some sort of contraction in a deuterostome's body axis pole separation without corresponding shortening of the longitudinal field lines [or inclination of the surface field vectors]? It is almost as if an eel-shaped animal underwent body axis shortening, but with the recalcitrant longitudinal field lines refusing to cooperate with a reduction in length. Latitudinal field lines would not be much affected in any case.

As a final consideration, there is evidence that geometrically-deployed sclerite primordia can reemerge in disparate lineages at unpredictable times. Geometric placement of osteoderms in the crocodylomorph ‘scleritome’ gives alligators and crocodiles their distinctive armored look. Cretaceous titanosaurid sauropod dinosaurs such as *Saltasaurus* apparently reactivated a dermal scleritome of osteoderms (Depéret 1896), after a long Jurassic hiatus where such osteoderm ornamentation was absent or less well-developed.

This has led vertebrate paleontologists to speak of “intrinsic skeletogenic properties of the dermis… These skeletogenic properties are not always related to a particular mechanism of formation in osteoderms” (Cerda and Powell 2010). Morphogenetic field control provides the fundamental mechanism. Collagenous fibers representing the longitudinal field lines, the latitudinal field lines, and the surface-normal vectors (structural fiber bundles) are preserved and present in the osteoderms of *Saltasaurus loricatus*, which develop by means of metaplastic ossification whereby soft tissue is replaced by bone. Sbaglio’s Law would certainly apply to these vectors.

Longitudinal field lines typically dominate the toroidal morphogenetic system, as shown by the fact that the osteoderms in *Saltasaurus loricatus* are elongated, with the major axis of the ellipse aligned with a first order longitudinal field lines. Also, the spacing between lines of arrested growth (LAGs) are widest where they are aligned with the first order field lines on the lateral edges of the osteoderm, and decrease to a minimum at the dorsal and ventral edges of the osteoderm (aligned with the minor axis of the ellipse). Three orthogonal axes of fiber bundles have also been reported from the ossicles of the Antarctic ankylosaur *Antarctopelta oliveroi*. Bundling of surface vectors can be seen in Cambrian scleritomes as well, where *Wiwaxia* sclerites are observed occurring in “bundles” (Smith 2014).

In their paper on *Saltasaurus loricatus*, Cerda and Powell (2010) discuss “deep homology”:

> As has been proposed by Hill (2006) for all vertebrates, the common growth pattern in the osteoderms of two non-related dinosaur groups as titanosaurs and ankylosaurs is an example of deep homology in vertebrates.

What they call “deep homology” is referred to here as a torologous relationship. Such torologous relationships span the divide between the vertebrates and the invertebrates. Amanda Lepelstat and her coauthors rightly attributed the torologous relationships among the dentition of early ‘ostracoderm’ fish, semionotid fish, pycnodont fish, teleost fish, and Paleozoic tetrapods to “control of sclerite/tooth position by an ectodermal morphogenetic field” (Lepelstat et al. 2010). This field control extends to external body coverings as well, and indeed the “outside-in” theory of teeth and dermal denticles (collectively called odontodes) has been confirmed at the expense of an “inside-out “ theory of the origin of external dermal denticles. Donoghue and Rücklin (2014) claim that “the ‘inside-out’ hypothesis must be rejected… [the] phylogenetic distribution of teeth and dermal denticles shows that these odontodes were expressed first in the dermal skeleton, but their topological distribution extended internally in association with oral, nasal and pharyngeal orifices, in a number of distinct evolutionary lineages." There seem to be few departures from the general rule of morphogenetic field control for odontodes, although a few exceptions are known. One strange case involves the dental tubercles of the acanthothoracid placoderm armored fish *Romundina*, where the rosette-shaped tubercles evidently grew from the center outward to form the rosette, a dental element that evidently served as crushing dentition (Rücklin and Donoghue 2015).

The most striking case of apparent reactivation of a scleritome morphogenetic field (Yang et al. (2014) call it "the reactivation of a dormant genetic machinery") is in a bizarre species of deep-sea vent gastropod. *Crysomallon squamiferum*, the scaly-foot gastropod, was discovered in 2001 living on the central Indian mid-oceanic ridge, associated with black smokers at the Kairei deep-sea vent field (Warén et al. 2003). The snail has a normal dorsal shell, but the foot of the snail is quite out of the ordinary. It is covered with sclerites composed of the iron sulfide minerals pyrite and greigite. This strange scleritome might seem to be unique, but it is important to recall that the radula (as seen in snails and chitons), itself a miniature scleritome, is also composed of iron-bearing minerals. The case of *Crysomallon* provides direct confirmation that the radula is indeed an anterior section of the scleritome with miniature sclerites, the radular teeth, with the *Crysomallon* foot sclerites serving as the $0 < |x| < a$ counterparts to the $b < |x| < c$ sclerites of the radula.

Crysomallon is able to construct an iron scleritome with relatively large sclerites along with a calcareous scleritome consisting of essentially one sclerite, its ordinary snail shell. This demonstrates flexibility of the morphogenetic field with regard to biomineralization, and its utility in facilitating various types and compositions of sclerites, sometimes within the same animal. Superimposition of multiple types of sclerites may be a possibility. I predict here the discovery of a stem group fossil mollusk that has an external skeleton consisting of both iron and calcareous sclerites of comparable size, perhaps occurring in a geometrical array, as part of a single complex scleritome. These examples reflect an element of truth in Erasmus Darwin's motto *e conchis omnia* ("from shells come all things"), which we might modify, to acknowledge the importance of the scleritome, to *ab exiguo conchas omnia* ("everything from small shelly fossils").

Left unstated at this juncture is the physical basis for the morphogenetic field. It is not some mysterious force but rather first appears in each individual by the binding of maternal RNAs to the new embryo's surface at the time of fertilization. Not surprisingly, considering the Cambrian conundrum regarding gene regulatory network kernels, maternal RNA researchers lament that "significant gaps remain in our mechanistic understanding of the networks that regulate early mammalian embryogenesis, which provide an impetus and opportunities for future investigations" (Lei et al. 2010). The field set up by the maternal RNAs provides the missing mechanism, as this is what sets up the initial morphogenetic field. By a mechanism still under investigation, the field remains at or near the surface of the organism through all ontogenetic stages, even during the transition from unicell to multicellular embryo.

Let's now consider further the newest tetrapod class, the Paramphibia. The unique jaw and punctate tooth morphology of the paramphibian *Permodiadonta* shares an odd mix of characteristics with fish, amphibians and reptiles. This mixture of traits precludes placement of the new species into any of these well-known vertebrate groups. In addition to punctate teeth (unusual in a tetrapod), there is a particularly strange feature visible in *Permodiadonta's* jaw—morphogenetic field lines that alternately converge and distend (Fig. 1.13) as they run across the edge of the jaw (as revealed by placement of the animal's dentition). Another way of saying this is that the zahnreihe Z-spacing is rhythmically variable. This strange configuration of zahnreihen (considered here to be proxy for the animal's morphogenetic field) reflects a body form that is as unique for vertebrates as the twisted-spindle morphology of the strange *Helicoplacus* is for Phylum Echinodermata. As helicoplacoids are placed in their own class (Class Helicoplacoidea), the placement of *Permodiadonta* in its own tetrapod class (Paramphibia) is amply justified by the available evidence.

Almost all reptiles show rows of "replacement" teeth; these rows are called zahnreihen. The cause of rows of teeth in reptiles and other vertebrates is sufficiently puzzling in evolutionary and developmental ("evo-devo") terms to lead DeMar (1972, p. 438) to lament that "mathematical studies of the organization of dentitions are not likely to fully reveal causes." Zahnreihen are in fact expressions of morphogenetic fields that control vertebrate dentition. We have here a torologous relationship with the mollusk radula and the conodont apparatus, in the $b < |x| < c$ scleritome zone. DeMar (1972) nevertheless takes pains to disavow the possibility that a morphogenetic field might in some way cause zahnreihen tooth rows: "*Zahnreihen*… are probably not fundamental in a causational sense… [they] are without causal reality… [and are] unreal in a causational sense." DeMar's (1972) denial of the possibility of torologous relationships speaks to a curious obstinacy when faced with facts difficult to reconcile with a biologist's preconceptions.

It seems safe to infer that the presence of a morphogenetic field can strongly influence development and morphological change. As noted earlier, morphogenetic fields (or progenitor fields; Davidson 1993) can be traced back to an initiation at the fertilization event, namely the organization of maternal RNAs over the surface of the fertilized egg cell membrane. Once we begin to observe and interpret this aspect of biological reality, namely, that there is ontogenetic information contained in membrane pattern (Wells 2014), we can begin to appreciate that there are influences on the morphology of creatures beyond that of nuclear DNA. As Shapiro (2011) put it:

> Like the man searching for his key under the lamppost, we currently focus our thinking about heredity almost completely on DNA sequences… we should never forget that not all heredity involves the transmission and interpretation of nucleotide sequences in DNA and RNA molecules. To date, all studies of genetically modified organisms have required an intact cell structure for the introduction of new genetic information by DNA or nuclear transplantation. So there is no unequivocal empirical basis for believing the frequent assertion that DNA contains all necessary hereditary information.

Not only will a proper understanding of morphogenetic fields and zahnreihen provide us with new tools to understand both the genesis of body form and macroevolutionary change, it will also help us to understand the relationship between odd changes to the morphogenetic field and the appearance of new higher taxa. It will also help us to reject false concepts of evolutionary gradualism and associated misconceptions surrounding our understanding of macroevolution.

During the beginning of what might be called the ‘punctuated equilibrium era’ in paleontology, DeMar (1972) made reference to cracks in the edifice of evolutionary gradualism: “If it [be] necessary to invoke evolutionary gradualism, then it would not be possible to evolve gradually to either of these [zahnreihen] spacings without passing through spacings that would cause [maladaptive] gaps in the tooth row.” de Ricqlès and Bolt (1983, p. 22) were later to add, in their analysis of the puzzling nature of zahnreihen as applied to jaw morphology: “We would emphasize… that this descriptive usefulness of zahnreihen does not imply a particular ontogenetic and/or functional mechanism. Elucidation of such mechanisms is a separate problem.” The time has arrived to deal with this mechanism problem. Analysis of the significance of morphogenetic fields reveals that zahnreihen are far more than merely successive rows of replacement teeth.

This point is underscored by the enigmatic Triassic tetrapod *Xenodiphyodon petraios*, where we see the six anterior monocuspid teeth responding to a primary zahnreihe that runs roughly parallel to the jaw, and the tricuspid, molarized three posterior teeth responding to zahnreihen that run at nearly right angles to the primary zahnreihe. This unique and curious configuration shows that *Xenodiphyodon* (Family Xenodiphyodonidae) has zahnreihen running across the surface of its jaws. Zahnreihen are not merely parallel lines but form a sheet-like network where the lines appear, in *Xenodiphyodon*, to form a strictly orthogonal grid.

For the best image of a sheet-like network, however, we must return to creatures of the Cambrian Explosion. The description of the armored kinorhynch-like scalidophoran worm *Eokinorhynchus rarus* takes on special importance in this regard (Zhang et al. 2015a, b). *Eokinorhynchus rarus* was recovered from the *Anabarites trisulcatus*-*Protohertzina anabarica* Assemblage Zone at Xinli and Xixiang sections in South China, an early Cambrian (535 million year old) occurrence that is close to the very beginning of the Cambrian Explosion. In the morphology of *Eokinorhynchus rarus* we can clearly see the importance of the morphogenetic field (Fig. 1.15).

Recovering this spectacular fossil was not an easy task; it required the acetic acid maceration of over a half a ton of limestone. *Eokinorhynchus rarus* is ornamented with numerous, geometrically placed small spines and scattered larger, rose thorn-shaped spines. Morphogenetic field control is evident, with transverse and longitudinal bands representing the latitudinal and longitude field lines, respectively. Sclerite size increases dramatically in the mouth region, following the shark torology of big oral sclerites as opposed to molluscan torology of tiny radular sclerites.

Fig. 1.15 *Eokinorhynchus rarus*, sketch of a spiny kinorhynch-like worm from the beginning of the Cambrian Explosion; **a** *dorsal view*; **b** *ventral view*, **c** *right lateral view*. Artwork by Dinghua Yang, Nanjing Institute of Geology and Palaeontology, used here per Creative Commons CC-BY license. Scale bar = 1.8 mm

Nevertheless, with *Eokinorhynchus* there are potential torologous links to mollusks and possibly arthropods as well. Instead of having a row of large spines along its dorsal (sagittal) midline, it has two roughly centrally placed rose thorn spines on either side of the sagittal midline. The placement of these large spines is highly reminiscent of the sclerites that remained after the Williston Law reduction in sclerite number to create a bivalve on the pattern of a clam, an ostracode (seed shrimp) or a bradoriid (Cambrian bivalve crustacean evolutionarily convergent on the Ostracoda). In this pattern of bivalve development, a left and a right sclerite (similar to what is seen on the back of *Eokinorhynchus* as the rose thorn spines) become the right and left valves of the clam. This is in contrast to the brachiopod case, where the head and tail large sclerites are combined to form the bivalve shell.

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Chapter 2
Christmas Tree Stromatolite

> *Why not go out on a limb? Isn't that were the fruit is?*
> Frank Scully (1892–1964)

Abstract What causes the unique shape of the Christmas tree stromatolite *Jacutophyton*? Branching in *Jacutophyton* appears to be controlled by both shade avoidance and by metazoan perturbation of the microbial mat at the edge of the stromatolite. Evidence suggests that heliotrophism in Proterozoic stromatolites is a real phenomenon.

Stromatolites are layered community fossils formed by accumulated successive layers of mineralized microbial mats or biofilms. These biofilms are typically bacterial in nature but this is not always the case (Awramik and Riding 1988). Cloud (1988) referred to stromatolites as "organo-sedimentary structures" to emphasize that they reflect an intimate interaction between life processes (biofilm growth) and sedimentological processes (layered sediment accumulation).

"Stromatolite" is thus a hybrid term of the type so useful in the Earth sciences. Another example is "time-rock unit", used to describe all of the rocks deposited within a particular time interval. We may speak of the Cretaceous Period (a discrete unit of time), and also speak of the Cretaceous System (the body of all the rocks formed during the Cretaceous Period). The Cretaceous System is thus a time-rock unit.

Stromatolites have the longest geological range of any type of fossil that is visible to the naked eye. Some Proterozoic stromatolites reach the size of mountains. Non-living geological processes can form structures that greatly resemble stromatolites. Abiogenic domed or columnar sedimentary structures have been called "stromatoloids" (Dahanayake et al. 1985). Therefore, attempts to interpret ancient stromatolites must proceed with care. In most cases, however, whenever stromatolites are encountered in shallow marine or freshwater strata, their interpretation as having been formed by microbial biofilms is very likely correct and uncontroversial. When filamentous microbial fossils are present (as when the rocks are silicified to form chert), the evidence is clear that the stromatolite was formed by biofilms. Such microfossils, however, are typically difficult to preserve as fossils owing to their tiny size. Nevertheless, larger scale textures in stromatolites can

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provide evidence for their derivation from biofilms. For example, characteristic fenestral patterns form in stromatolites due to oxygen bubbles formed by photosynthesis becoming trapped between the biofilms (Wilmeth et al. 2015). These distinctive features provide evidence for both a biogenic and photosynthetic nature for the biomats that formed the stromatolite. 'Biofilm' is thus an appropriate name as it emphasizes an ability to trap gas.

Biofilms are extensive and widespread for most (about 5/6th) of geological time, but it would be a mistake to dismiss biofilms as merely representing primitive life forms. Recent results suggest that the microbial species in modern multispecies biofilms collaborate to develop "enhanced resistance to antibiotics" (Denison and Muller 2016). Alternatively, single-strain biofilms are formed by the bacterium *Pseudomonas aeruginosa* by killing off other strains in the immediate vicinity (Oliveira et al. 2015). Clearly there is more complexity here than might initially meet the eye.

With their long geological history, it is no surprise that a variety of different shapes or forms of stromatolites have existed over the billions of years of Earth history. *Platella* is a unique stromatolite group that forms an elongate dome, oriented in the direction of the ebb and flow of tides (Keller and Semikhatov 1976). *Platella* was evidently sculpted by daily tidal flow, alternating currents that formed the distinctive elongate/parallel ridges of this stromatolite group (Cevallos-Ferriz and Weber 1980). Some columnar stromatolites bend into unidirectional currents, and others develop a sinusoidal curve in their column axis that has been hypothesized to track the position of the sun (Awramik and Vanyo 1986). The latter result was used to calculate the length of the Proterozoic year at 400 ± 7 days. It has also been used to argue that the Earth had an essentially normal tilt on its axis, in other words, the obliquity of the Proterozoic ecliptic was not significantly different from current values (McMenamin 2004). Awramik and Vanyos' (1986) claim of heliotropism in Proterozoic stromatolites has been vigorously debated; however, the specimens used as counterexamples also display the sine wave pattern (Williams et al. 2007). To date the inferred heliotropism has not been falsified.

Kusky and Vanyo (1991) advocated using stromatolite heliotropism to refine paleotectonic continental plate reconstructions. Williams et al. (2007) countered that the "acceptance and use of such data are premature… further data and tests relevant to the sinusoidal growth model are desirable." Kusky and Vanyo (1991) cited Horodyski (1983) regarding the stromatolites of the Mesoproterozoic Belt Supergroup of Glacier National Park, Montana, noting that inclinations occur in these stromatolites, but left open the question of "whether stromatolite inclination could be a result of heliotropism or currents" (Horodyski 1989).

Horodyski (1983) published a sketch of inclined stromatolites of the Altyn Limestone near Appekunny Falls in Glacier National Park. His Fig. 5E is reproduced here as Fig. 2.1. Although he does not assign them to group, the stromatolites in Fig. 2.1 are "highly elongate and are shown on a joint surface oriented perpendicular to the direction of elongation," and thus should be assigned to the stromatolite group *Platella*.

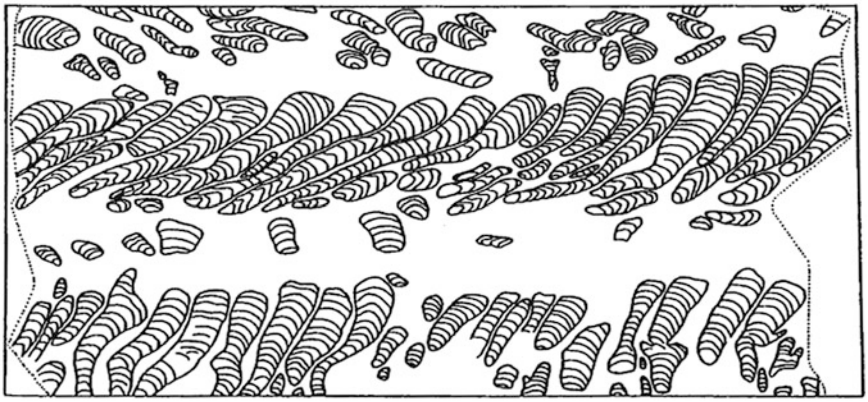

Fig. 2.1 Horodyski's (1983) sketch of *Platella* stromatolites of the Altyn Limestone near Appekunny Falls, Glacier National Park, Montana. Height of outcrop seen in section (along a joint surface perpendicular to the elongation of the *Platella* columns) is approximately 1.6 m. Reprinted from *Precambrian Research*, volume 20, R. J. Horodyski, "Sedimentary geology and stromatolites of the Middle Proterozoic Belt Supergroup, Glacier National Park, Montana," pages 391–425, 1983, with permission from Elsevier

There does not at first glance appear to be a sinusoidal pattern to the inclinations of the *Platella* stromatolites in Fig. 2.1. To help with the analysis, it is important to recall that *Platella* lives in an intertidal environment. This explains the odd elongated shapes of its columns. *Platella* columns are mechanically sculpted to have this shape by the continual, daily ebb and flow of the tides.

Note that intertidal depositional environments are highly erosive. Tidal sediment transport is constantly wearing away at any obstructions in the path of the abrasive sediment in motion. Flat bedrock surfaces, slightly inclined toward the sea, often result from this process and are called wave-cut terraces. As a general rule, interruptions in the continuity of sedimentation (diastems or hiatuses) become more frequent as one gets closer to the shoreline, and less frequent as one moves offshore and into deeper, quieter water.

Inhabiting a very shallow water environment, *Platella* is thus subjected to a great deal of erosive scour; its environment is so highly erosive that the preservation of *Platella* is probably more the exception than the rule. A close inspection of Fig. 2.1 shows horizons of *Platellas* inclined at odd angles with respect to horizons above and below. One may discern four separate horizons of *Platella* stromatolites in Horodyski's (1983) sketch.

If we separate these four *Platella* horizons, they each may be fitted to a sinusoidal curve as shown in Fig. 2.2. Erosional gaps separate the four horizons, as would be expected in *Platella's* erosive intertidal environment. The period of the vertical sine wave is approximately 114 cm. A dramatic confirmation of the accuracy of this reconstruction, and the interpretation of the pre-erosional morphology of the stack of Montana *Platellas*, is seen in a book chapter by Serebryakov (1976) that includes

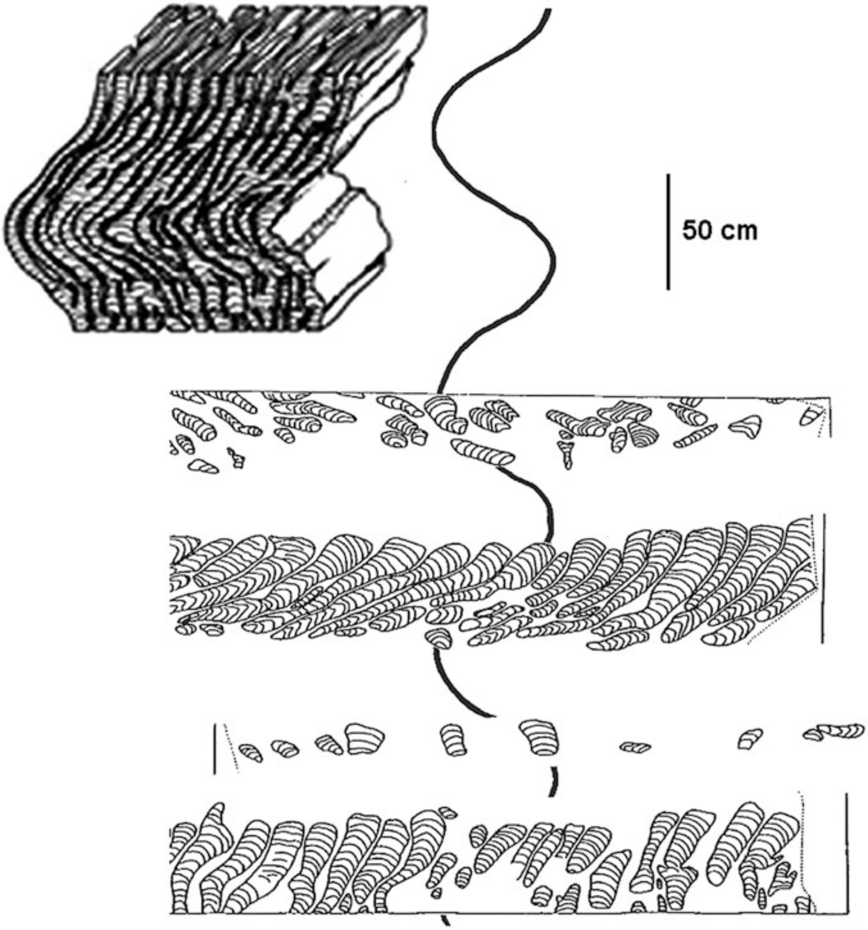

Fig. 2.2 *Platella* stromatolite horizons of the Altyn Limestone, Montana, with their inclinations fitted to a sinusoidal curve interpreted here to represent the track of stromatolite heliotropism in *Platella*. The inclination fitting has revealed four hiatuses, diastems or gaps in deposition in the Altyn stromatolite succession. The period of the sine wave is approximately 114 cm. Inset image to the upper left is modified from Serebryakov's reconstruction (1976, his Fig. 1, p. 324) of sinusoidal *Platellas* from the Proterozoic (Riphean) Debengda suite of the Olenek Uplift of the Siberian Platform. If you look closely at the inset, you can see evidence for at least four brief gaps in deposition, as in the Altyn case but with only minor loss of the sequence erosion or non-deposition. Stromatolites from Montana and Siberia are drawn to scale. Scale bar = 50 cm

a block diagram (modified here as the upper left inset in Fig. 2.2) of sinusoidal *Platellas* from the Proterozoic (Riphean) Debengda suite of the Olenek Uplift of the Siberian Platform in eastern Siberia. Serebryakov nicely shows the wave shape of the Olenek *Platellas*. Very interestingly, and this is likely not mere coincidence, the period of the sine wave in the Siberian stromatolites is exactly the same as that of the Montana *Platellas*, namely, 114 cm. The comparison is even closer than it looks at first—if you look closely at the inset, you can see in the block diagram evidence for at least four brief gaps in deposition, as in the Altyn case only with not as much of the sequence lost to erosion or non-deposition. This close comparison further supports the interpretation of a heliotropism signal in the *Platellas*, assuming as seems reasonable that the two sites were at roughly similar paleolatitudes at the time their respective stromatolites were deposited. Siberia and western North America were close to one another in the Rodinia supercontinent, but this assumption requires further evaluation by using modern plate reconstructions to assess stromatolite heliotrophism, which will effectively run the research program of Kusky and Vanyo (1991) in reverse.

The θ angle (Vanyo and Awramik 1985; the theta value used in their calculations is θ = 19.6°) of the Altyn Limestone stromatolites (θ = 56°) is too large to provide a realistic measure of Earth-Sun-Moon dynamics, thus it appears that the *Platella* ridges were not just bending into the light but that their ridges (linear columns) were actively migrating toward the sun. Unfortunately, this will greatly complicate the study of stromatolite heliotropism because it introduces an additional parameter. Calculations of orbital dynamics will only work if you can assume that no stromatolite column sideways axis-shifting migration has taken place, or if you are able to calculate the rate at which the stromatolites have migrated (as opposed to simply leaned into) the sun. I will show below that stromatolite migration is a very real phenomenon. There does not seem to be evidence for stromatolite migration in the work of Awramik and Vanyo (1986), so we can accept their results as provisionally valid.

We must of course consider alternate explanations for the phenomenon. Changes in nearshore current directions might be invoked to explain the sinusoidal wave, but stromatolites tend to bend into currents, and current surge in *Platella's* intertidally influenced environment runs parallel to the long axes of the columns, not perpendicular to it. Mars' obliquity can change up to 60°, but this takes place over the course of millions of years (Touma and Wisdom 1993), and proposing that the Earth's obliquity could change by this amount over the course of a season would be too much to ask of orbital mechanics to say the least.

Stromatolite diversity peaks in the Proterozoic about 1.25 billion years ago, and drops off rapidly afterwards. This sharp decline has been attributed to the rise of grazing animals (Awramik 1971). By the Cambrian, global stromatolite diversity is reduced by at least 20 %, and today stromatolites form only where high salinity or other environmental factors inhibit grazing aquatic animals that would otherwise disrupt the biofilm fabric and prevent stromatolites from forming. Interestingly, it has been argued that stromatolites make a brief comeback as "disaster forms" in the Early Triassic, during global biotic recovery after the horrific Permo-Triassic mass extinction (Schubert and Bottjer 1992). Domal stromatolites from the Cambrian and later, including the splendid Cambrian "cabbage heads" at Lester Park, Saratoga Springs, New York, often show evidence of animals burrowing between and through the stromatolitic layers.

Stromatolites come in three main shape varieties: domal, columnar and conical. Awramik and Semikhatov (1979) use the term "stratiform stromatolite" for stacked planar biofilm laminae with little or no synoptic relief. Stromatolite morphogenesis has been attributed to the operation of the four variables of the Kardar-Parisi-Zhang (KPZ) non-linear stochastic partial differential equation (Grotzinger and Rothman 1996). The surface fractal or Eden growth model has also been used to describe the growth of microbial cluster colonies and accumulation of material around the edges of the microbe clusters (Family and Vicsek 1985). Although it may be possible to describe some stromatolites by means of these four processes, a Laplacian nonlocal growth model better describes most stromatolites (Batchelor et al. 2003).

As their name suggests, domal stromatolites take on the form of an inverted salad bowl. Their internal structure consists of domal layers. Columnar stromatolites, in side view, appear as straight or gently curving columns consisting of tall stacks of arched laminae. Conical stromatolites are quite different in form when compared to the other two types. They project upward a considerable distance from the sea floor; in stromatolites, the distance they project above the sea floor is called their synoptic relief. Conical stromatolites consist of steep-sided, conical laminae that often have a disturbed zone at the top of the cone. In a longitudinal cross-section through the exact center of a conical stromatolite such as *Conophyton*, the stacked disturbed zones resemble a zipper running down the center of the stacked cones.

Perhaps the strangest and most wonderful of all stromatolites is *Jacutophyton*. It often occurs in the same Proterozoic stratigraphic sequences as does *Platella*. *Jacutophyton* is nicknamed "Christmas Tree stromatolite" because of its branch configuration—a conical core surrounded by inclined columnar branches that resemble the branches of a fir tree (McMenamin 1982). Figure 2.3 shows a comparison between the columnar stromatolite *Baicalia*, the conical stromatolite *Conophyton*, and the conical stromatolite with branching sub-columns *Jacutophyton*.

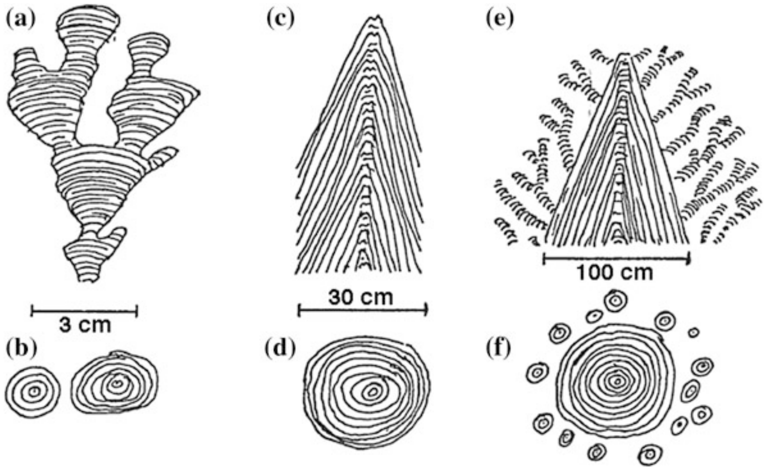

Fig. 2.3 Three different groups of Proterozoic stromatolites. Each is shown in longitudinal and transverse section. **a**, **b**, *Baicalia*, a branching columnar stromatolite, scale bar = 3 cm; **c**, **d**, *Conophyton*, a conical stromatolite, note disturbed central axis, scale bar = 30 cm; **e**, **f**, *Jacutophyton*, a conical stromatolite with branching sub-columns, scale bar = 100 cm

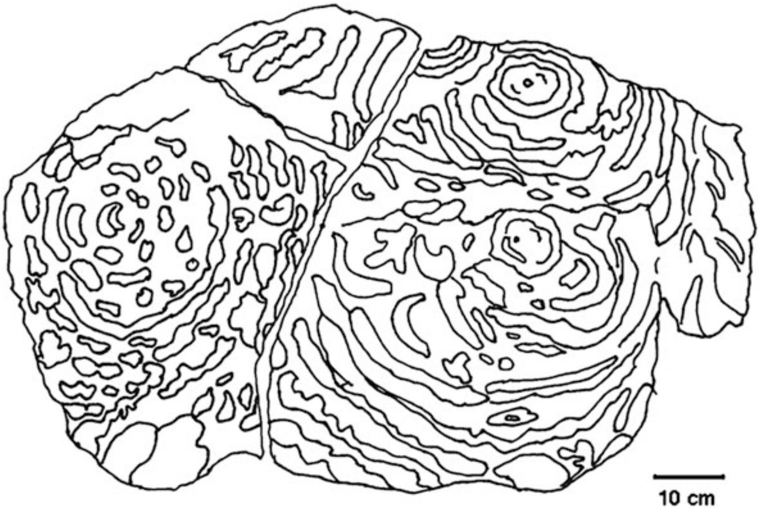

Fig. 2.4 *Jacutophyton sahariensis* from the Atar Formation of Mauritania. Three stromatolite central cores are visible. Note the petaloid shapes of the satellite stromatolites surrounding the central cones. The specimen on the *left* has the petaloid fabric reaching all the way to the center of the stromatolite. Scale bar = 10 cm

In life, *Jacutophyton* resembled a *Conophyton* surrounded by low synoptic relief satellite columns. The branching columns are typically elliptical in transverse cross-section, but in *Jacutophyton sahariensis* from the Atar Formation of Mauritania, Africa, the branches form low ridges (resembling miniature concentrically-curved *Platellas*; Fig. 2.4) that give *Jacutophyton sahariensis* a petaloid aspect (Swart et al. 2009) in transverse section that somewhat resembles a dental tubercle of *Romundina*. The overall impression of a living *Jacutophyton sahariensis* would be similar to that of flower of the titan arum *Amorphophallus titanum*, with its towering central spadix (up to 3 m tall) surrounded by a spathe that resembles large curving petals. In transverse cross-section the curved branches of *Jacutophyton sahariensis* do seem to radiate out from the central cone in waves, much like curved, nested flower petals.

Jacutophyton is abundant in the Late Proterozoic Gamuza Formation near the town of Caborca in Sonora, México. Stratigraphically beneath the Gamuza Formation is the famous Clemente Formation, known for its very ancient Ediacaran fossils (McMenamin 1996). An unanswered question about *Jacutophyton* is just how this stromatolite acquired its odd shape. Stromatolites are usually either domal, columnar or conical, not combinations of the above. Columnar stromatolites will sometimes transition stratigraphically upward into domal stromatolites, and vice versa, but combinations of stromatolite types at the same level (i.e., same lamina) are rare.

If we follow a single lamina of *Jacutophyton*, as seen in longitudinal cross-section (Fig. 2.3e), passing from left to right we encounter one small column, then a second, then a third, then the conical upward projection of the core of the *Jacutophyton*, then three small columnar stromatolites on the far side. Field observations show (Swart et al. 2009) that "branches [in *Jacutophyton*] initiate along a single lamina of the central cone."

We can answer this question of how *Jacutophyton* acquired its unusual shape by means of an analysis of its growth. A stromatolite is generally thought to begin as an upward rumple, pustule or irregularity in an otherwise roughly planar microbial mat or biofilm on the sea floor or on the floor of a lake. Microbial mats typically develop this surface roughness. This texture can be preserved in the sedimentary rock record in both Precambrian and post-Cambrian strata (Bailey et al. 2006), and when it does preserve, it is called "elephant skin texture," a type of microbially induced sedimentary structure. The faster a biomat grows, the rumplier its surface becomes as the mat expands and is forced to wrinkle like a rumply rug. Light is attenuated fairly rapidly in water, and rumples that bow upwards have access to detectably more sunlight than the surrounding flat mat. Light-hungry microbes migrate to the top of the lumps. These upward facing wrinkles thus often become the establishment sites of new stromatolites.

Interestingly, microbial mat wrinkles are comparable to those formed experimentally on 3-D layered gel models of the cortical convolutions of the brain. The artificially produced cortical crenulations are remarkably similar to those of actual brains. According the authors (Tallinen et al. 2016), the "placement and orientations of the folds" in the simulated brain "arise through iterations and variations of an elementary mechanical instability modulated by early fetal brain geometry." This suggests an intriguing mechanical similarity to elephant-skin texture and the crenulations of the brain. In the former, biomat layering probably helps influence the appearance of the mat crenulations.

With cyclical (in some cases daily) growth of the mat microbes, successive layers are formed over the rumple and this upwardly domal mat becomes, with successive layers, the stromatolite. If the stromatolite is broad and wide, it becomes a domal stromatolite; if it is smaller and button-shaped it will form a columnar stromatolite of the successively accreted layers. The synoptic relief of the dome- or column-forming mat may only be a few millimeters. It is the numerous accreted laminae that form the dome or tall column as seen in longitudinal cross section (Figs. 2.3a, c, e). Conical stromatolites are typically the only type of stromatolites that show, in life, significant synoptic relief, and their actively-growing cones project some distance upward into the water column. A patch of sea floor hosting conical stromatolites would resemble a parking lot covered with green traffic safety cones.

A *Jacutophyton*-colonized sea floor would be somewhat similar, except that one or more concentric rings of low curved ridges or small domes would surround each cone. Looking closely at the later, they would not have a perfectly symmetrical domal profile, but rather would lean away from the vertical and erect central cone. What could lead to such a curious configuration?

A stromatolite-like structure known as a thrombolite (its name refers to its clotted internal structure) is common in late Precambrian and early Paleozoic marine strata. A thrombolite is essentially the same thing as a stromatolite, and both are classified as a type of microbialite. Each type forms in the same way by the sediment-binding activity of a biofilm. Thrombolites differ from stromatolites in

Table 2.1 Types of calcimicrobe structures

Type	Internal fabric	References
Stratiform stromatolite	Planar laminae	Awramik and Semikhatov (1979)
Stromatolite	Domed laminae	Awramik and Semikhatov (1979), Kennard and James (1986), Shapiro (2004)
Thrombolite	Mesoclots	Kennard and James (1986), Shapiro (2004)
Dendrolite	Clusters	Shapiro (2004)
Leiolite	Not recognizable	Riding (2000), Shapiro (2004)

that the laminated internal fabric has been profoundly disrupted by the activities of burrowing animals (Kennard and James 1986). The stromatolite-to-thrombolite transition appears to be part and parcel of the overall decline during the late Proterozoic of stromatolite groups, a process that has been attributed as noted above to the rise of burrowing and grazing animals that appear millions of years before the Cambrian Explosion.

In addition to stromatolites and thrombolites, other microbiolites are known including dendrolites (characterized by calcimicrobe clusters; Shapiro 2004) and leiolites (internal fabric not discernible; Riding 2000). Table 2.1 summarizes the main types of microbiolites.

I propose here that *Jacutophyton* represents a conical stromatolite that has experienced the early stages of what might be called "thrombolitization." In this scenario, burrowing animals of the sea floor impinged against the edge of an undisturbed *Conophyton*, at the perimeter circle where the cone of the stromatolite begins to rise up from the sediment-water interface. This occurred because the earliest metazoans are thought to have been undermat miners, feeding on organic matter underneath the biofilm, and their mat-mining routine was impacted when, while burrowing in the horizontal plane, they ran into the nearly vertical wall of a conical stromatolite. The small animal would try to climb the column, turn around, or make some other unfamiliar maneuver, and in so doing would cut through, thin, or otherwise disrupt the mat at the base of the cone.

These minor disruptions would initiate new, smaller satellite stromatolites that began to form columns. The columns are inclined away from the main conical core, and thus form tilted branching columns, as they seek areas away from the shade of the main cone. This causes the satellite domes to progressively migrate away from the main cone, as the diagram in Fig. 2.5 indicates.

Let D_o be the initial distance of the satellite stromatolite from the axis of the main conical center of a *Jacutophyton*. With successive growth stages (Fig. 2.5), the distance of the satellite stromatolite from the central axis at interval n is

$$D_n = D_o + xn \tag{2.1}$$

with n equaling the number of growth increments elapsed on the main cone (as shown by successive stromatolitic laminae), and x the distance that the satellite

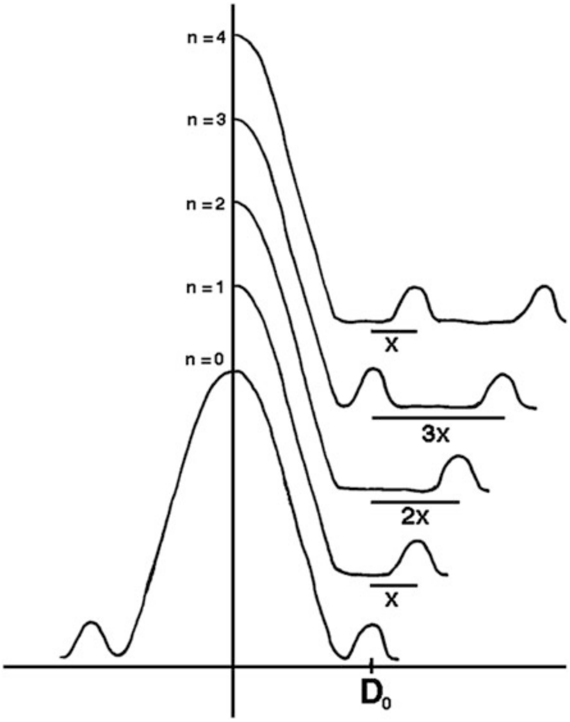

Fig. 2.5 Growth of the *Jacutophyton* stromatolite. This diagram shows four growth intervals of the stromatolite, from n = 0 to n = 4. These intervals can be considered as accretionary stages in the upward growth of the stromatolite. D_o is the initial distance of a nascent satellite stromatolite from the central cone axis. The satellite stromatolite moves a distance x away from the main axis with each growth increment (n). When it reaches a critical distance from the axis G, a new satellite stromatolite forms at a distance D_o from the central axis

cone migrates away from the axis with each iteration. G is a particular critical distance from the main stromatolitic axis. In Fig. 2.5 the G value equals the initial distance D_o plus three sideways growth increments x, or $G = D_o + 3x$. When:

$$D_n > G \tag{2.2}$$

a new satellite stromatolite is generated at a distance D_o from the main axis. Successive "waves" of satellite stromatolites thus migrate away from the main central cone, and this is what gives *Jacutophyton* its Christmas Tree shape as seen in longitudinal cross section. The stacked branches are satellite stromatolites migrating away in increments from the shade of the central cone as they add their incremental layers.

It would be interesting to discover what controls the value of x between the various forms of *Jacutophyton*. Higher values of x will generate more horizontal branches, and lower values of x will generate more upright or vertical branches. One might plausibly speculate that the value of x is inversely correlated to light intensity at any particular site. Low light levels might cause the satellite stromatolites to move away from the main cone more rapidly in order to capture whatever light is still available, hence a higher x value.

It is easy to imagine how this might happen. Filamentous cyanobacteria will tend to congregate on the side of the satellite stromatolite apex that is away from the main cone. This is virtually the same effect that explains the disturbed zone (longitudinal section "zipper") seen in the axis of a typical *Conophyton*. The apex of the cone gets the most light, and microbes congregate there in such numbers that they form a tiny, very rumpled patch of elephant skin texture right at the tip of the cone. This explains the laminae disturbance that runs up through the exact center of a *Conophyton* (Fig. 2.3c).

We might also speculate on the critical distance value G. It might very well also be light dependent, but could also be influenced by other factors such as the intensity of disruption of the microbial mat by animals burrowing in the vicinity of the stromatolite. This latter consideration might also influence whether the *Jacutophyton* forms branches or, alternatively, forms "petals" as in *Jacutophyton sahariensis*.

The beautiful form of *Jacutophyton* thus provides us with a glimpse into the dynamics between Proterozoic stromatolites and early animal burrowers as the marine biosphere approached a critical point marking the beginning of the Cambrian. *Jacutophytons* of the Gamuza Formation are like fancy hats for a "graduation party" marking the transition from Microbe World to Metazoan Planet.

Jacutophyton sahariensis occurs in the Atar Formation of Mauritania. The Atar Formation is approximately 800 million years old, and this is an early date for putative animal burrowers; however, the putative burrowers may have been living in a symbiotic relationship with *Jacutophyton sahariensis* that led to the unique petaloid shape. This would be in contrast to complete destruction of the laminar fabric as in subsequent thrombolites. Figure 2.4 shows three *Jacutophyton sahariensis* stalks, in one of which the petaloid fabric goes all the way to the center of the stromatolite as seen in transverse section. In this case the conical core appears to be lost, suggesting perhaps that the burrowers were in fact capable of disrupting even the central cone. The morphology of the *Jacutophyton* to the left in Fig. 2.4 is approaching that of a thrombolite. Table 2.2 shows the relationship between internal fabric and burrowing disturbance in organo-sedimentary microbialites.

Table 2.2 Fabric and burrowing disturbance intensity in organo-sedimentary microbialites

Organo-sedimentary structure	Fabric	Burrowing disturbance intensity
Stratiform stromatolite	Planar laminated	Low
Oncolite	Concentrically laminated oncoliths (oncoids; Shapiro 2004)	Low
Conophyton, *Platella*	Laminated	Low
Jacutophyton	Branched to petaloid	Intermediate
Thrombolite	Clotted	High
Dendrolite	Clusters	Variable

Jacutophyton provides a fine example of morphogenesis, where a well-defined geometrical form (conical stromatolite) undergoes a dramatic shape change (to Christmas Tree Stromatolite) by application of a new outside influence (burrowers), leading to a new regime of morphogenesis (satellite stromatolites). With increased disruption the Christmas Tree shape changes to a petaloid configuration, and finally to a thrombolite where the mound or dome shape reappears, but without any internal laminae because the biomats have been destroyed by intensive burrowing.

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Chapter 3
Archaeocyath Mixotrophy

> *Not everything that counts can be counted, and not everything that can be counted counts.*
>
> Albert Einstein (1879–1955)

Abstract Analysis of the feeding strategy of the bizarre fossil *Retilamina* shows that this archaeocyath represents the earliest known example of animal mixotrophy in Earth history. *Retilamina* is estimated here to have been approximately 80 % photoautotrophic and 20 % heterotrophic.

We will now cross the Cambrian boundary to further explore this topic of morphogenesis, particularly as it applies to animals participating in the Cambrian Explosion. Many evolutionists desire to draw out the Cambrian Explosion interval to 58 million years or more (Lipps 2004), in an attempt to salvage conventional, gradualist evolutionary theory. As we will see in Chap. 7, these attempts run afoul of sampling bias. The extremely rapid morphogenetic change of archaeocyaths in the Early Cambrian challenges any sort of gradualistic explanation for the boundary event. Charles Darwin was quite averse to any abrupt or catastrophic explanation for natural phenomena, and allowed this predilection to sway his scientific judgment. For example, Darwin (1874) rejected a catastrophic explanation for the large clast conglomerates of Bermuda, arguing that gradualist arguments had "generally succeeded in explaining such phenomena by simpler means." Darwin was wrong about this, however, and we now know that the coarse Bermudan conglomerates are the result of hurricanes (Ager 1993).

Archaeocyaths are a strikingly beautiful group of sponge or sponge-like organisms that lived in reef communities known as archaeocyath-calcimicrobial bioconstructions of the Early Cambrian shallow sea floor (Gandin and Debrenne 2010). Most archaeocyaths consist of a cup inside of a cup, with skeletal material between the two walls (Fig. 3.1). Their porous inner and outer walls are connected either by porous walls known as septa or irregular skeletal plates and rods known as pseudosepta or taeniae. In transverse cross section, the septa look like the spokes of a wagon wheel. The archaeocyath body has a hollow central cavity surrounded by the inner and outer skeletal walls. After the initial growth stages, these walls are porous.

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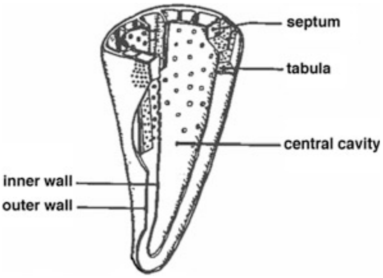

Fig. 3.1 Archaeocyath morphology. Cut-away diagram showing the structure of a typical Lower Cambrian archaeocyath. Diameter of cup 2 cm

Archaeocyaths first appear in the Tommotian Stage of the Early Cambrian (a.k.a. Cambrian Stage 2). They reach their maximum diversity during the Atdabanian-Botomian Stages (Cambrian Stage 3), go into a rapid decline in the subsequent Toyonian Stage (Cambrian Stage 4), and by the end of the Cambrian ("Stage 10") are represented by only a single species, *Antarcticocyathus webberi*. The Botomian Stage has been called the "Age of Archaeocyaths."

At their peak in the Atdabanian-Botomian, archaeocyaths are global in distribution. Their diversity at this time attains hundreds of genera (Rowland and Hicks 2004), an astonishing number for the time. This growth in the number of genera represents the fastest genus-level diversification in the entire fossil record. As such, archaeocyaths represent the criterion example of the Cambrian Explosion. Their body form ranges from the bizarre, flattened *Retilamina* to the strange tree-like *Yukonensis*. Figure 3.2 shows a sketch of the variability in archaeocyath body plan, ranging from flat *Retilamina*, to modular *Salairocyathus*, to transversely annulate forms such as *Orbicyathus*, to horsetail-shaped *Yukonensis*.

The porosity of archaeocyath cups is one of their most striking characteristics. The porosity is so extreme in some genera that the inner and outer walls, septa, and tabulae resemble spindly frameworks not unlike the geometrical framing that supports the windowpanes in an old-fashioned greenhouse.

Is the overall shape and geometric porosity of archaeocyaths the result of a complex morphogenetic field? A number of archaeocyath genera and species would seem to support the notion that a morphogenetic field is at work in construction of the archaeocyath cup (in terms of geometry, a horn torus) and its modifications

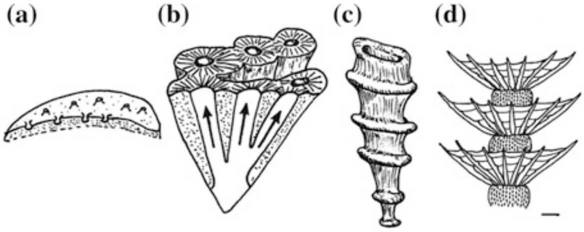

Fig. 3.2 Variability in Archaeocyath Form. **a** *Retilamina*, a sheet-like to domal encrusting form; **b** *Salairocyathus* (*Polystillicidocyathus*) *erbosimilis*, a pseudoserioid modular form, *arrows show* presumed direction of passive exhalant flow; **c** *Orbicyathus*, an annulate form with elliptical transverse section; **d** *Yukonensis*, a form that develops corolla spines. Scale bar = 2 mm

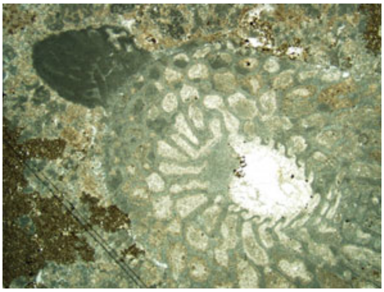

Fig. 3.3 Geometrical pores or syrinx facets of Lower Cambrian *Pseudosyringocnema*. Note sparry calcite fill of central cavity and parasitic archaeocyath at *upper left*. Width of view approximately 8 mm

(Debrenne and Zhuravlev 1992). The geometrical pores or syrinx facets of *Syringocnema* and *Pseudosyringocnema* (Fig. 3.3) look like 3D nets resembling the Fresnel diffraction pattern.

The tabular structure of *Dictyosycon* sp. from the Asiatic Altay Sayan fold belt looks like a crystal model showing bonds between atoms. The flattened *Okulitchicyathus discoformis* looks like a pancake with concentric markings, resembling part of the biconvex electrostatic field lines of electron diffraction experiments. Strangest of all, however, is the inner wall structure of the archaeocyath *Tercyathus altaicus* from the Sanashtykgol Suite of Sayan. The structure resembles a nonlinear chemical oscillator such as the Belousov-Zhabotinsky reaction more than it does any familiar biological structure (Vologdin 1957). Archaeocyath morphogenesis is evidently being controlled by systemic rules, perhaps involving some sort of patterning parameters (Newman and Bhat 2008). Morphogenetic field control is clearly at play here, with all three axes (X-, Y- and Z-axis) of the field contributing to morphogenesis. It is as if the morphogenetic field has gone out of control, penetrating deep into the interior of the animal rather than existing as a mere surface patterning grid.

Sometimes it is best to begin with an examination of the strangest cases in order to access more information about overall system dynamics. By consulting the helpful online resource *Archaeocyatha—A Knowledge Base*, we see that arguably the strangest of all archaeocyaths is the flattened genus *Retilamina* (Fig. 3.2a). *Retilamina* has completely lost its chalice shape, and thus lies prostrate on the sea floor. The ordinary cup shape of the archaeocyath body plan has been split and flattened. In *Retilamina* the outer wall forms an upper crust and the inner wall surface is attached to the sea floor. McMenamin and Hussey (2015) reported a new occurrence of *Retilamina* from New Jersey and considered how the bizarre creature fed. *Retilaminas* form a cavity space on the sea floor underneath their flat skeleton. The New Jersey *Retilamina* developed a strange finger-shaped projection (Fig. 3.4) into this cavity space. This projection is called a stolon, and it appears to be the same phenomenon seen in typical archaeocyaths called tersoid exothecal outgrowths (Rowland and Hicks 2004), except that instead of projecting outward from the outer wall as in tersoid exothecal growths, stolons project inward from the inner wall. McMenamin and Hussey (2015) argued that:

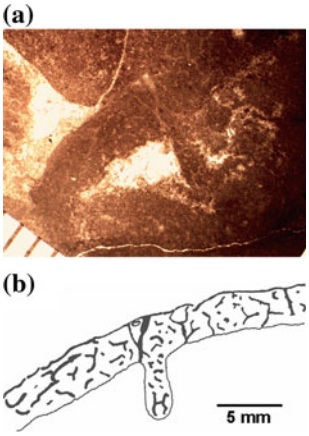

Fig. 3.4 *Retilamina* grows a stolonic projection beneath its skeletal sheet. **a** Photomicrograph showing stolonic projection; **b** Sketch of the skeletal sheet and stolonic projection. Associated fauna on this slide includes brachiopods, hyoliths, and radiocyaths. Archaeocyathan carbonate, lower Leithsville Formation, Franklin, New Jersey, field sample 1 of 10/19/89. Scale in **a** in mm

> The passive filter-feeding method of typical, erect cup-shaped archaeocyaths would function poorly at the lower current speeds encountered in *Retilamina's* sea floor surface habitat. *Retilamina's* stolonic projections into cavity spaces pose an additional problem, as flow velocity would presumably be even lower in these cryptic spaces (perhaps 0.1 mm/s or less). Cavity water would be lacking in sufficient suspended particulate food matter to permit efficient filter feeding. We propose that *Retilamina* fed by direct absorption of dissolved nutrients released by the breakdown of organic matter in cavity pore spaces, supplemented by capture of mobile substrate bacteria as they moved through pore fluids toward the sediment-water interface.

Investigation of *Retilamina's* morphology and the factors that led to its strange baüplan may provide new insights into its trophic strategy. Continued research located a specimen of *Retilamina* from México that strongly supports the above interpretation of trophic strategy in the New Jersey *Retilaminas*. The Sonoran archaeocyath has well developed vertical slats, like venetian blinds that have been opened, on its underside. These seem well-suited to conduct materials from the substrate upward into the flat archaeocyath.

In archaeocyaths, the space between the inner and outer walls is called the intervallum. The part of each wall that faces into the intervallum is called the carcass. The well-developed slats on the Mexican *Retilamina* occur on the inner wall carcass. *Retilaminas* from other areas also show the slat-like development, but rarely as strongly as in the Sonoran specimens. Slat development appears to be most pronounced where the *Retilamina* surface curves abruptly, as can be seen in the image on the *Knowledge Base* entry for this genus. In *Retilamina*, recall that, as the *Knowledge Base* puts it, the "upper wall corresponds to the outer wall and the lower wall to the inner wall." What I have called slats in *Retilamina* are referred to in the *Knowledge Base* as "vertical intervallar structures."

We may now synthesize some key observations. First, in the not-as-strongly-curved part of the *Retilamina* skeletal sheet in the *Knowledge Base* photograph (Fig. 3.5), the underside of the *Retilamina* is festooned with brushy calcimicrobes (Pratt 1984; Shapiro 2004) belonging to the genus *Epiphyton*. The *Epiphytons* are

Fig. 3.5 *Retilamina amourensis* sketch showing pendant *Epiphyton* clinging to inner wall. *Epiphyton* is largely absent where the *Retilamina* skeletal sheet is arched. Illustration redrawn from a photograph of *Retilamina* in the online resource *Archaeocyatha—Knowledge Base* Scale bar = 1 mm

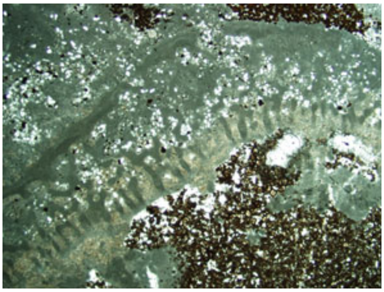

Fig. 3.6 *Retilamina* sp., archaeocyathan limestone. Note the concentration and height of vertical slats (vertical intervallar structures) where the skeletal sheet is arched. Puerto Blanco Formation, Unit 4, Cerro Rajón, Sonora, México, field sample MM-82-54, same slide as previous photomicrograph. Width of view 8 mm

smaller or absent where the *Retilamina* is strongly arched, and this is also where the vertical intervallar slats are developed.

These same features can be observed in the Sonoran *Retilaminas*. Slats appear where the skeletal sheet is arched and *Epiphyton* is absent (Fig. 3.6). Well-developed *Epiphyton* appears where the sheet is not arched and where slats are absent (Fig. 3.7).

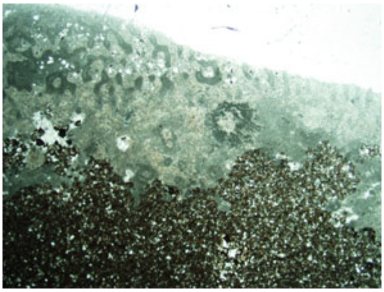

Fig. 3.7 *Retilamina* sp. with pendant calcareous alga *Epiphyton* sp. (just to the right of center of the photomicrograph). Archaeocyathan limestone, Puerto Blanco Formation, Unit 4, Cerro Rajón, Sonora, México, field sample MM-82-54. Width of view 7 mm

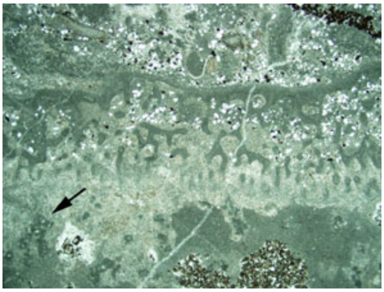

Fig. 3.8 *Retilamina* sp., archaeocyathan limestone, Puerto Blanco Formation, Unit 4, Cerro Rajón, Sonora, México, field sample MM-82-54. *Renalcis* sp. clusters are visible in the *lower left* of the photomicrograph (*arrow*). *Renalcis* to the right of the arrow appears to be boring cavities into the micritic (lime mud) matrix. Note the sparry pocket close to the *Renalcis* with oxide-coated euhedral carbonate crystal rhombs. Width of view 7.3 mm

Small clusters of the round calcimicrobes *Renalcis* appear beneath the skeletal sheet where slat development is present but weaker (Fig. 3.8).

Another key observation is that, in the vicinity of the stolonic projection in the New Jersey *Retilamina*, there is are prominent vertical intervallar structures in the immediate vicinity of, next to, and even within the stolonic projection (Fig. 3.4). Some of these vertical intervallar structures run vertically all the way across the *Retilamina* intervallum.

Several opinions have been expressed regarding *Retilamina's* trophic strategy. Some researchers have controversially (Manne 2004; Forsey 2013) argued for photomutualism in *Retilamina*, due to its association with the calcimicrobes *Renalcis* and *Epiphyton*. These frequently occur beneath the skeletal sheet (Hicks and Rowland 2005). The calcimicrobes are reasonably inferred to have been photosynthetic. As noted above, our group argued that *Retilamina* fed by direct absorption of dissolved nutrients (osmotrophy) released by the breakdown of organic matter in cavity pore spaces, supplemented by capture of mobile substrate bacteria as they moved through pore fluids toward the sediment-water interface.

The correct interpretation of *Retilamina's* feeding is as follows. This archaeocyath used all three trophic strategies: photosymbiosis, osmotrophy, and capture of bacteria. Where its skeletal sheet arches upward and forms slats on the inner wall like grills on a vent, osmotrophy and/or bacterial capture is taking place. Nutritious gases bubbling up from the substrate moved through the *Retilamina* intervallum, directed upward by the slats, and (like a miniature version of a stratigraphic trap for natural gas) were trapped in the arch, where the animal absorbed them at its leisure. "Chimney pores" appear at the crest of the arch (Figs. 3.5 and 3.6) to increase the rate of flow and rate of food absorption or capture. Where the skeletal sheet was smoother, and where calcimicrobes festooned the underside of the inner wall, it is very likely that some type of nutrient exchange took place, probably involving photosynthesis-derived sugars from *Epiphyton* and *Renalcis*. The calcimicrobes were protected by the *Renalcis* skeletal sheet, and yet were still able to receive sufficient light in their cryptic habitat. The slats did not develop in this part of the archaeocyath wall, indeed the inner wall here is much reduced, thus the Venetian blinds were removed and light passed through unhindered. Thus we have here the earliest good evidence in the fossil record for *mixotrophy*, a mixed trophic strategy that combines nutrients acquired from different sources. *Retilamina* was a multitask feeding factory.

It is possible to estimate the relative proportions of the various trophic strategies employed by *Retilamina* by measuring the amount of its inner wall carcass devoted to photosymbiosis or osmotrophy/bacterial capture, respectively. I will keep this calculation very simple and restrict it for now to a single specimen, the *Retilamina* illustrated in *Knowledge Base* (Fig. 3.5). Similar specimens are shown in Debrenne and James (1981).

This analysis will make the simplifying assumption that a given area of *Retilamina* sheet will absorb the same amount of nutrient regardless of feeding method. Concerning the *Retilamina* trophic intake in calories, let T_{obf} represent the proportion of food resource taken in by osmotrophy-bacterial feeding, and T_{cap} represent the proportion of food resource taken in by calcareous algal photosymbiosis. Thus:

$$T_{obf} + T_{cap} = 1.0 = 100\,\% \tag{3.1}$$

In Fig. 3.5, 9 mm of the inner wall near a prominent bend show evidence for slats and represents T_{obf}. On either side of the skeletal sheet bend, 13 mm (left side) and 20 mm (right side) of the inner wall is festooned with *Epiphyton* and/or *Renalcis* (the two may be ecomorphs of the same species and/or diagenetic taxa; Pratt 1984). Savarese and Signor (1989, p. 546) illustrate a flat-sheet *Retilamina* with no prominent bends, and in accord with the model presented here the underside/inner wall of their *Retilamina* is evenly colonized with *Renalcis* clusters.

Let W_t denote the total length of the inner wall as seen in section, W_{obf} the length of the inner wall with bend and/or slats, and W_{cap} the length of inner wall with growths of *Epiphyton* and *Renalcis*. Thus:

$$W_t = W_{obf} + W_{cap} = 42\,\mathrm{mm} \tag{3.2}$$

$$T_{cap} = W_{cap}/(W_t) = 33/42 = 0.785 = 79\,\% \tag{3.3}$$

$$T_{obf} = 1 - \ T_{cap} = 1.0 - 0.785 = 0.214 = 21\,\% \tag{3.4}$$

As a rough estimate, then, *Retilamina* received 39 % of its trophic resources from photosymbiosis, and 61 % from osmotrophy and digestion of bacteria. Where the skeletal sheet bowed up, it served to concentrate upward flow, and where it was flat, it served as a solar panel. Another way of saying this is that *Retilamina* was approximately 80 % photoautotrophic and 20 % heterotrophic.

This approximate result makes possible an interesting comparison with a modern group of marine mixotrophs, scleractinian photosymbiotic corals. When these corals are healthy and not bleached, their internal, photosymbiotic zooxanthellae (microbes such as the dinoflagellate *Symbiodinium*) provide 90 % of the host coral's nutrient requirements. This symbiotic food source is a great boon to corals in a nutrient-depleted reef water habitat (Stanley 2006). *Retilamina* was slightly more heterotrophic than a modern coral, with an autotrophy to heterotrophy ratio of 80 to 20 % as opposed to 90 to 10 %, respectively. The comparison is quite apt, as *Retilamina* also inhabited a reef or reef-like habitat that likely also experienced nutrient-deficient waters.

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Chapter 4
Environmental Convergence

> *The huge iguanodon might reappear in the woods, and the ichthyosaur in the sea, while the pterodactyl might flit again through the umbrageous groves of tree ferns.*
>
> Charles Lyell (1797–1875)

Abstract Why do characteristic features of the Proterozoic sea floor reappear in Mesozoic lake strata? The reappearance is a case of environmental convergence, where very similar environmental/ecological settings appear at widely separated moments in geological time. In this and other cases, non symmetry in the fossilized biofilms is key to recognition of ancient organo sedimentary structures. These can appear at any time or in any place when aquatic conditions permit.

Several great unanswered paleontological questions surround our study of the Ediacaran fossils. One asks: “How did these creatures feed?” A second asks: “How were these soft bodied creatures preserved in such exquisite detail?”

Regarding the first question, there are several alternate perspectives. The conflict between them has not yet been adequately resolved. The first of these is the Garden of Ediacara hypothesis, which states that the Ediacaran marine biosphere hosted large benthic organisms that lived uniquely low on the food chain, surviving by means of osmotrophy, photosymbiotic autotrophy, chemosymbiotic autotrophy, or similarly autotrophic ways of making a living. A growing case can be presented for both Ediacaran photomutualism and osmotrophy for at least some of the organisms based on their “large, flattened, quilted” morphologies (Forsey 2013). One point in favor of the Garden of Ediacara is the apparent absence of large and aggressive predators in the Ediacaran biosphere.

The alternate perspective sees the Ediacaran marine scene in more modern terms, with a sea floor surface much as today, colonized primarily by filter feeders, biofilm grazers and primary and secondary carnivores. We could call this the Filter Factory hypothesis. The Garden of Ediacara and Filter Factory hypotheses are not mutually exclusive, of course. There were surely both large osmotrophs and early filter feeders on the sea floor in the late Proterozoic. The investigation revolves around the relative importance of these two main strategies. Did a uniquely peaceful, “soft

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path" marine paleoecology characterize Ediacaran times? Or was it the familiar Tennysonian predator prey situation, "nature red in tooth and claw," with a larger number of ecological guilds, albeit in a somewhat unfamiliar format?

In an attempt to resolve the dispute between the Garden of Ediacara and Filter Factory alternatives, Rahman et al. (2015) attempted to "test between competing feeding models" for the triradial Ediacaran *Tribrachidium heraldicum*. Rahman et al. (2015) correctly noted, contrary to some claims (Clapham and Narbonne 2002; Clapham et al. 2003), that we do not "really have any good evidence of suspension feeding in organisms of this time period." Using computational fluid dynamics, Rahman et al. (2015) concluded that "the external morphology of *Tribrachidium* passively directs water flow toward the apex of the organism and generates low velocity eddies above apical 'pits.'" Rahman et al. (2015) conclude that their results provide the first evidence for suspension feeding in the fossil record. The radially symmetric shape of *Tribrachidium* would allow the putative passive suspension feeding to work for currents approaching from any direction. Furthermore, the results were consistent for all the current velocities tested in the model. As passive flow suspension feeding is also inferred for archaeocyaths (Balsam and Vogel 1973), if confirmed the *Tribrachidium* result would support the idea of trophic continuity across the Proterozoic Cambrian boundary. As such, this would represent a 'test' of feeding strategy that would favor the Filter Factory hypothesis at the expense of the Garden of Ediacara hypothesis.

It is now time to evaluate the *Tribrachidium* experiment by taking a look at *Tribrachidium's* closest relatives, lumped together in a clade known as the Triradialomorpha. Whereas the mesh skeleton of archaeocyaths is ideal for sieving water for particulate food, it is less clear how a suspension feeding strategy could be effective for a non porous structure such as the relatively low relief *Tribrachidium* shield. The triradiate *Tribrachidium* relatives *Albumares brunsae* (Fig. 4.1) and *Anfesta stankovskii* have the triradial pattern but, as the Rahman and coauthors note, no putative food capture pits, and the Rahman modeling results would not necessarily apply to these forms.

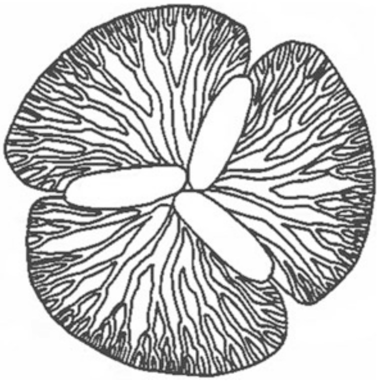


Fig. 4.1 *Albumares brunsae* from the Ust Pinega Formation, Summer Shore, White Sea, Russia. Diameter of fossil 10 mm

More serious is the problem posed by *Tribrachidium's* closest relative, *Gehlingia dibrachida*. *Gehlingia* is a bilaterally symmetric frondose form that lies prostrate on the sea floor. Its overall shape is very distinct from the triradial *Tribrachidium*, but the basic structure consisting of separate branches with bifurcating branchlets, and "thumb structures" branching off the main trunk of each branch, indicate close biological affinity (McMenamin 1998) with *Tribrachidium*. *Gehlingia* is essentially a *Tribrachidium* that has lost one of its arms and has straightened out the other two in response.

To proceed with the comparison between *Tribrachidium* and *Gehlingia*, we must first ascertain the correct position of the thumb structures in *Tribrachidium*. Some reconstructions show the three thumb structures situated on the inner part of the curve of each main branch; others show the thumb structures occurring on the outer edge of the curve of each main branch. Rahman and others paper (their Fig. 4.1) shows the thumb structures in the latter configuration. Which configuration is correct?

We may answer this question by a close inspection of *Gehlingia* (Fig. 4.2). On *Gehlingia* right side (top side in Fig. 4.2), the thumb structure is on the outer edge of the main branch curve (ignoring the distal tip of this branch that curves away from the midline). On *Gehlingia* left side, the thumb structure is on the inner edge of the main branch curve. Thus, the thumb structure in both *Gehlingia* and *Tribrachidium* may be positioned on either side of the main branch trunk. This suggests that the main trunks in both genera may be flipped over interchangeably top to bottom, and still function well for the organism in terms of acquiring food. This would be a decidedly unusual flexibility in a suspension feeding animal. For example, if you take a filter feeding sea anemone, turn it over, and smash its tentacles into the sediment of the sea floor, it is no longer going to function very well as suspension feeding organism. In any case, there is no evidence indicating that the secondary branches in *Tribrachidium* represent tentacles.

Rahman and coauthors argue that the food particles would collect via "gravitational settling" into the pits—low velocity zones—and that the design is "more

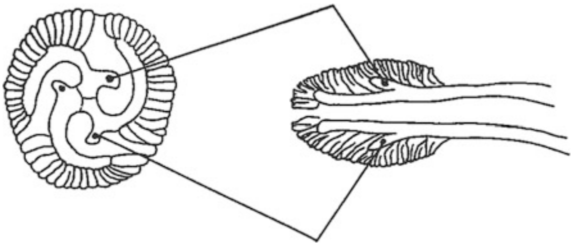


Fig. 4.2 *Gehlingia* and *Tribrachidium*. Comparison between the Ediacaran genera *Tribrachidium* (*left*; diameter 1 cm) and *Gehlingia* (*right*; length 8.1 cm). The two tie lines connect homologous structures (i.e., bodily structures sharing a common descent or ancestry) informally referred to as "thumb structures." The correlation indicates that these two Ediacarans are closely related in spite of their radically different (triradial versus bilaterally symmetric) body forms

efficient in stronger currents." The stronger currents they note are at 0.2 m/s. At this current speed, it seems that any food particulates in suspension would stay in suspension. The food would be washed away, not collected into the shallow pits. The relief on *Tribrachidium* is simply too subdued to be of much help for effective filter feeding.

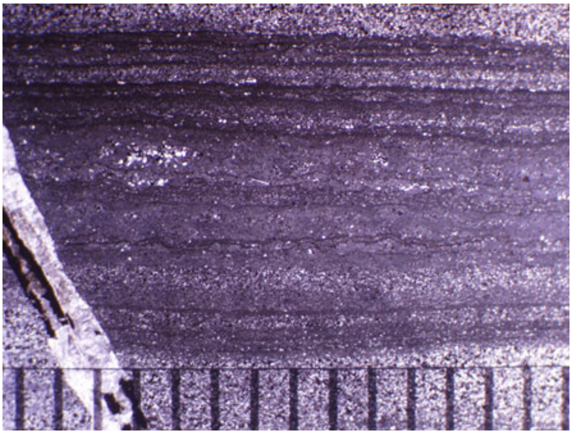
The pits ("apical pits") occur at and near the junction of the main branches and the thumb structures. Presumably they would also occur in the analogous space near the thumb junction in *Gehlingia*, but here, due to *Gehlingia's* frondose rather than triradial configuration, the flow dynamics would be completely different.

Singer et al. (2012) showed that Ediacaran fronds become oriented in the direction of current, and argued that this was a point favoring the interpretation of an osmotrophic feeding strategy in Ediacaran fronds. The flow tends to slow down and distribute itself evenly over the surface of the frond, supposedly allowing the frond to more easily absorb dissolved nutrients from the current flow. The localization of flow claimed by Rahman et al. (2015) to occur near the top center and pits of *Tribrachidium* would be an even better than a frond for slowing down and perhaps even reversing the current, thus allowing more opportunity for absorption of dissolved nutrients, without the difficulty that currents may not be sufficiently impeded to allow suspended particulate food matter to settle out. Thus, the results of Rahman et al. (2015) can be interpreted as favoring an osmotrophic feeding strategy in *Tribrachidium*.

This is particularly so considering that *Tribrachidium's* closest relative, *Gehlingia*, assumes a frondose shape and thus demonstrates an apparent affinity for osmotrophic feeding in this part of the Triradialomorpha clade. Whether or not *Tribrachidium* and *Gehlingia* were photoautotrophic or chemoautotrophic is difficult to ascertain with the evidence currently in hand. However, both genera have a relatively high surface area due to flattening of the body, especially around the lateral edges. Also, both genera are known to inhabit shallow marine waters near storm wave base and thus well within the marine photic zone, as shown by their occurrence in thin bedded sandstones that develop wave and current ripples. Possible photosymbiosis is entirely plausible for both genera. Indeed, *Tribrachidium* has a body shape very comparable to thalli of the liverwort *Marchantia polymorpha*, and *Gehlingia* has a passing resemblance to the leaf of the angiosperm *Philodendron*.

The second question we began with in the text of this chapter, namely, how were primarily soft bodied Ediacaran fossils preserved in such exquisite detail, is a question of taphonomy. The word "taphonomy" is derived from the ancient word for tomb, and indeed refers to the science of burial and preservation of dead organisms. The taphonomy of Ediacarans remains a great puzzle. Most of the organisms involved had what were apparently soft, flexible integuments. Nevertheless, they are preserved in organic poor shales, limestones and even sandstones that would ordinarily be unlikely to host the preservation of such fossils because bacterial growth in these sediments is not inhibited by factors such as, say, low oxygen levels as in organic rich shales. The soft integuments of deceased Ediacarans should have been quickly consumed and destroyed by bacteria.

Fig. 4.3 Biomats as seen in thin section from the Proterozoic Mina el Mesquite Formation of Sahuaripa, México. The wrinkly biomats are clearly visible in the center part of the photomicrograph. Note calcitic vein to lower left showing several generations of crystallization, one of which had an iron rich (opaque) phase. Field sample 6 F16 40 J; collected by J.H. Stewart. Scale in mm



Nevertheless, the impressions of such striking forms as *Dickinsonia*, *Yorgia, Spriggina* and *Tribrachidium* are preserved as high detail impressions of a type that would ordinarily be associated with rare Lagerstätten such as at Chengjiang. This type of preservation among Ediacarans is widespread on a global scale and occurs at virtually all the sites where larger Ediacaran body fossils have been recovered.

The conundrum experienced a breakthrough when Gehling (2004) proposed the "death mask" hypothesis. It has been recognized for some time that Precambrian seas were characterized by sea floor biomats or biofilms of global extent, and Ediacarans are often associated with these biomats (Seilacher 1999). These are the same biofilms that by successive incremental layers formed stromatolites. Figure 4.3 shows examples of biomats as seen in thin section from the Proterozoic Mina el Mesquite Formation of Sahuaripa, México.

Gehling (2004) suggested what seemed at first to be an unlikely scenario. Instead of the Ediacaran remains being destroyed by the feeding action of bacteria, they were instead preserved by the action of bacteria, or more specifically, by mineralization of the biofilms that grew over the Ediacaran corpses. In Gehing's (2004) view, the films grew over the upper surfaces of dead Ediacarans, and then precipitated a thin layer of biominerals (perhaps comparable to a single stromatolitic lamina) that hardened the upper surface of the Ediacaran, like a thin film of wax, creating a "death mask" that held the organism's shape long after death. The death mask then allowed the soft Ediacaran to make a firm impression in the relatively coarse, sandy sediment of the next layer deposited.

Biofilms form over the remains of modern organisms, dead fish for example, and are associated with increased alkalinity of the soft tissue remains (Iniesto et al. 2015). Similar chemistry may have occurred inside dead Ediacarans that were covered by biofilms, and the Proterozoic case was unusually effective at preserving the body fossils in sharp detail.

Figure 4.4 shows a specimen of shale that has developed classic elephant skin texture. The curious thing about this specimen is that it's not a marine specimen of

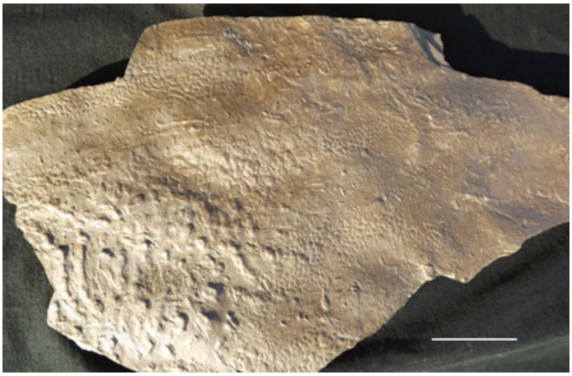


Fig. 4.4 Shale that has developed classic elephant skin texture from the Connecticut Valley Region, USA. Specimen and photograph courtesy Andrew Brodeur. Scale bar = 6 cm

Proterozoic age, but rather a fresh water, lacustrine specimen of Mesozoic age. Is this merely an indication that aquatic microbes, whenever provided with the opportunity to do so, will form biofilms on the bottom of a body of water? Or is there a deeper message here? In other words, can past conditions of the biosphere re establish themselves when favorable environmental conditions arrive?

There has been much recent discussion in paleontology about the concept of "ecosystem engineering" (Jones et al. 1994, 1997), the concept that organisms such as bioturbators modify their environmental surround to such an extent that it influences the availability of trophic resources for other species. McMenamin and Schulte McMenamin (1990) argued that burrowers had become so disruptive of the sea floor that new food resources appeared in the water column, thus encouraging filter feeders and leading to a major advance in ecosystem engineering (Erwin 2008). The new food resources helped to drive the Cambrian Explosion. This is linked to the idea that appearance of abundant skeletons in the Cambrian "does not coincide with the opening of a taphonomic window, but with a polyphyletic explosion in defense and biomineralization" (Caron et al. 2013).

As currently articulated, there is a sense with ecosystem engineering that the development of the biosphere through time is progressive, in the sense that once the biosphere acquires new capabilities there is no turning back to previous states. Certainly, the Hypersea concept of spread of terrestrial vegetation over the dry land surface represents ecosystem engineering on a grand scale. The Hypersea phenomenon induced a new geophysiological process called hypermarine upwelling, that is, the upward flow of mineral nutrients from the soil and regolith into the biosphere (McMenamin and Schulte McMenamin 1994). Hypermarine upwelling led to a massive expansion of terrestrial biomass and species numbers, and also delivered nutrients back to the oceans and estuaries. This led to the development of most major types of fish, including the ancestors of the tetrapods, and is the proximal reason that the Devonian has been referred to as the Age of Fishes. Nutrients from the first forests entered the shallow marine biosphere and apparently triggered a piscine evolutionary diversification.

Is it possible for the biosphere to return to earlier, less "engineered" or developed ecosystem states? The topic has a long history of discussion in the geosciences, some of it tongue in cheek. Charles Lyell, the preeminent geologist of his time, wrote in all seriousness in his seminal work *Principles of Geology* (1830–1833) that, should future environmental conditions permit, then "might those genera of animals return, of which the memorials are preserved in the ancient rocks of our continents. The huge iguanodon might reappear in the woods, and the ichthyosaur in the sea, while the pterodactyl might flit again through the umbrageous groves of tree ferns."

It is a striking concept that led to caricature by one of Lyell's contemporaries. Paleontologist Henry Thomas De la Beche is credited with the first paleoecological reconstruction. His 1830 painting *Duria Antiquior* (*Ancient Dorset*) showed marine reptiles, ammonites and other cephalopods inhabiting and interacting in an ancient sea. The work celebrates Mary Anning's fossil discoveries on the Dorset coast, and shows such detail that it even portrays the production of coprolites by the marine reptiles.

In *Duria Antiquior*, a large Jurassic ichthyosaur is shown biting down on the neck of a plesiosaur; this represents one of or perhaps the earliest artistic rendering of an ancient predator prey interaction. Interestingly, although English Jurassic ichthyosaurs were probably more suited to feeding on fish and cephalopods than on other marine reptiles such as plesiosaurs, subsequent research has shown that there was an apex predator Mesozoic marine reptile genus, *Dakosaurus*, that was indeed specialized for consuming other marine reptiles (Buchy et al. 2007). *Dakosaurus'* snout was shortened in accord with its feeding preferences, giving it a powerful bite (the genus name means "biter lizard") that is evolutionarily convergent on the shape of the skull of *Tyrannosaurus rex*.

De la Beche also inked a cheeky spoof of Lyell's inference from *Principles of Geology*. In an 1830 cartoon entitled *Awful Changes: Man found only in a Fossil State—Reappearance of Ichthyosauria*, a Professor Ichthyosaurus, wearing a splendid embroidered coat, has clambered out of the water onto a shoreline outcrop and is addressing an attentive audience of fellow ichthyosaurs. The Professor's pointer indicates a human skull preserved in the rock layers that serves as his podium. The Professor continues his talk: "You will at once perceive that the skull before us belonged to some of the lower order of animals; the teeth are very insignificant, the power of the jaws trifling, and altogether it seems wonderful how the creature could have procured food."

Levity aside, De la Beche alludes to several key paleontological concepts in his cartoon. First of course, he highlights the pitfalls of making paleoecological inferences based on limited data. As noted earlier in this chapter, it still seems puzzling how Ediacarans procured their food. Second, we see in the cartoon, in caricature form, Lyell's return of the Ichthyosauria. But these are not the same ichthyosaurs as those that lived in the Mesozoic. Rather, these ichthyosaurs are sentient beings capable of engaging in college level coursework! This implies both the concept of convergent evolution, and the controversial notion that intelligent life forms (once defined by Stephen Jay Gould as those creatures capable of discerning evolutionary history—Professor Ichthyosaurus apparently satisfies this requirement!) could reappear or even *had previously* appeared in the Earth's past. We will examine this last point further in a subsequent chapter. Lest I appear to be reading way too much into De la Beche's cartoon, note that the points raised here are among the most important and contentious issues in the Earth and planetary sciences.

For example, if environmental conditions comparable to those of the past reappear, will the "same" biota reappear? This would imply a sort of extended convergent evolution, where different lineages converge on what might be called "archetypal" forms of the past, having been induced to do so by a return of particular climate or other environmental conditions. The implications of a Platonic ur form in this situation are interesting to contemplate. Perhaps there are a limited number of ways of successfully doing particular things in biology. Nevertheless, does gradual Darwinian evolution have the requisite time to search all the possibilities before settling on the forms that function well (Conway Morris 2003)? This point alone constitutes a robust challenge to conventional notions of gradual evolutionary change by natural selection.

Can organisms themselves induce the return of particular environmental conditions? We could call this possibility *Environmental Convergence*. This in a sense would be driving the history of life backwards. Not only could the organisms themselves influence food supplies for other species, they could drive the environmental conditions surrounding them to a particular state. This would combine convergence of individual lineages, convergence of ecological guilds back to former states, and indeed convergence of the entire biosphere back to a former condition. Could feedback from a particular climate state lead to stabilization at a particular climate setting, modulated by a Gaia like control of the climate by the biosphere? This would indeed be environmental convergence extended to the entire surface of the globe. It is the apparent goal of environmentalists who would like to return the Earth's climate and environment to a previous, and supposedly more pristine, *state*.

Finally, can we predict the occurrence of particular local environmental conditions in extraterrestrial settings? The recent discoveries of myriad exoplanets as predicted by Cloud (1983) strongly suggests the possibilities of interplanetary convergences, should there happen to exist Earth like planets with sufficient water to host a flourishing biosphere.

Returning closer to home, let's now examine the possibility of environmental convergence between Proterozoic marine and Mesozoic lacustrine environments. To do so, we will focus on several specific sedimentological and paleontological features that can be easily observed in preserved strata. These features include size gradational mat pustules, tear drop structures, mat stabilized starved ripples, treptichnid trace fossils, and Ediacaran analogs.

Proceeding with this analysis will require the following assumption. This analysis assumes that the first three of these five sedimentological features are indeed the result of the growth and sediment binding action of microbial mats. Other explanations, for example, wrinkled non microbial clay films, abiogenic

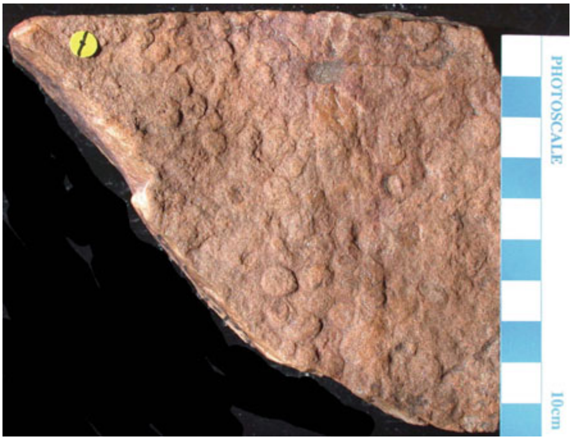


Fig. 4.5 Mat pustules from *Pteridinium* beds of the Nama Group, in Namibia. Scale bar in cm

runzelmarken, etc., are possible but are considered here to be less likely because of the *non symmetrical* nature of structures 1–3.

Let's first consider size gradational mat pustules. These structures can form today, as is seen in gas blisters in a modern biofilm at Tecopa Hot Springs, California (Cloud et al. 1974). Figure 4.5 shows a piece of late Proterozoic sandstone from the site of the famous *Pteridinium* beds of the Nama Group, in Namibia. This piece was observed during the famous Seilacher expedition to Namibia in 1993. The photograph shows the upper surface of the small slab, the top bedding plane surface. This surface is covered with low domal mat pustules. Note how the pustules increase in size as you move from left to right across the image. Figure 4.6 shows the relationship between pustule diameter and distance from an arbitrary reference line as shown on the image in the upper left.

Figure 4.7 shows a shaly siltstone specimen from early Mesozoic lacustrine beds of the Hartford Basin, South Hadley, Massachusetts. There is again a gradation in mat pustule size, with the larger diameter pustules again on the right side of the photograph. A plot of the data is seen in Fig. 4.8. Note that a curving trace fossil is seen on the Mesozoic specimen. The smooth contour along the edge of the

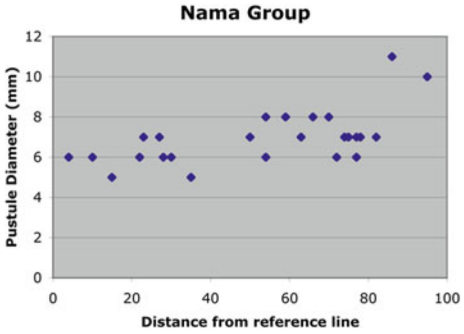


Fig. 4.6 Nama specimen; bivariate plot of relationship between pustule diameter and distance from an arbitrary reference line

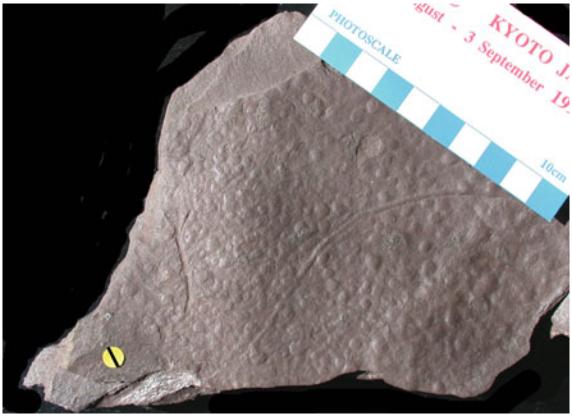


Fig. 4.7 Mat pustules from early Mesozoic lacustrine beds of the Hartford Basin, South Hadley, Massachusetts. Field sample 1 of 5/14/85. Scale bar in cm

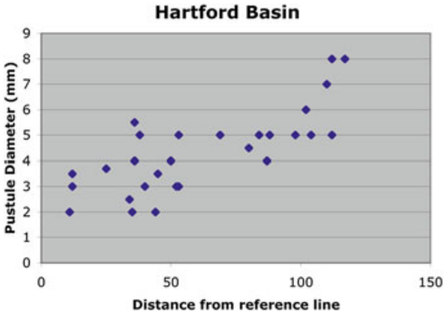


Fig. 4.8 Massachusetts specimen; bivariate plot of relationship between pustule diameter and distance from an arbitrary reference line

ichnofossil indicates that it is an undermat miner trace fossil. The burrowing invertebrate was apparently moving and feeding just underneath the flexible biofilm, pushing it up like a sheet of deformable plastic as it moved forward to feed on organic deposits.

Combining the two data sets of pustule diameters and distances from the reference line, and plotting the regression lines for each set of data (Fig. 4.9), we see that the regression lines are nearly parallel. The formula for the Nama regression line, and its R^2, is:

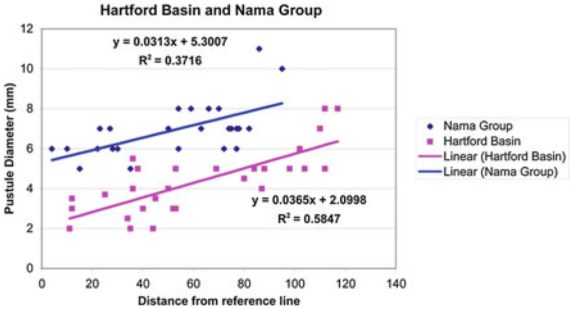


Fig. 4.9 Combination plot with regression lines calculated for both the Hartford Basin and Nama Group mat pustule size variation. Note the nearly parallel aspect of the two regression lines

$$y = 0.0313x + 5.3007 \tag{4.1}$$

$$R^2 = 0.3716 \tag{4.2}$$

The formula for the Hartford Basin regression line, and its R^2, is:

$$y = 0.0365x + 2.0998 \tag{4.3}$$

$$R^2 = 0.5847 \tag{4.4}$$

The slopes of the two regression lines are quite similar, averaging about 0.034. There is a hint here that biomat pustule populations can change size across a bedding plane surface in what may be a systematic fashion, that plots along a line with a calculated slope of 0.034. More data of course are needed to confirm this, but there is also the possibility that this slope value will remain roughly invariant for larger, marine biomat pustules and smaller, lacustrine biomat pustules. Whether or not average biomat pustule diameter may be correlated to the effective size of the body of water in which they are forming is an intriguing question that can inspire further investigation.

Figure 4.10 shows what I call teardrop structures from the late Proterozoic Clemente Formation, Sonora, México. These structures have a teardrop shape and are typically aligned with their long axes parallel. Whereas the mode of formation of mat pustules is fairly straightforward to understand—reminiscent of the Ediacaran death masks, they represent what might become the first lamina of a nascent stromatolite—the mode of formation of teardrop structures is currently unknown. They may represent some type of tool marking that was subsequently modified by overgrowth of the microbial mat in death mask fashion. In any case,

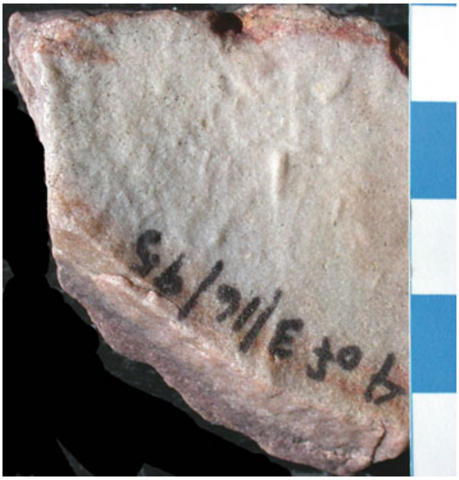


Fig. 4.10 Teardrop structures from the late Proterozoic Clemente Formation, Sonora, México. Field sample 4 of 3/16/95. Scale bar in cm

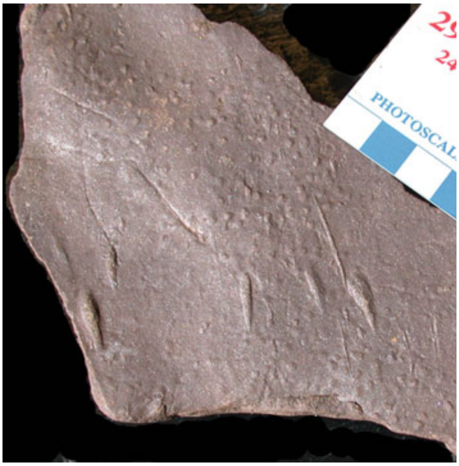


Fig. 4.11 Mesozoic teardrop structures, again from the Hartford Basin, Portland Formation, of South Hadley, Massachusetts. Field sample 2 of 4/10/86. Scale bar in cm

Fig. 4.11 shows well-developed Mesozoic teardrop structures, again from the Hartford Basin, Portland Formation, of South Hadley, Massachusetts. Here we see the teardrop structures co occurring with scattered, small mat pustules, all of about the same diameter, and thus not size gradational in this case.

Starved ripples are ripple marks that form on the bottom of a body of water when there is insufficient sand to form regular ripples and dunes. If preserved as sedimentary rock, starved ripples can lead to the preservation of sedimentary structures known as flaser bedding. The sand of starved ripples travels over a firm muddy substrate, similar to a mud flat surface only underwater. In some cases, the starved ripples may move over a microbial mat. When such ripples stop moving because ambient current velocity has decreased, the microbial mat will, in death mask fashion, grow up over the sandy ripples.

Ripple stabilization can happen to well fed sand ripples as well. Figure 4.12 shows mat stabilized ripples from Ediacara in South Australia with a *Tribrachidium* that had settled into the trough between the ripples. This specimen could be construed as evidence favoring the Rahman et al. (2015) hypothesis regarding *Tribrachidium* suspension feeding, as the trough between ripple crests would tend to be a lower velocity current setting where particulate food might tend to settle out. However, there are several alternate hypotheses to explain the position of the *Tribrachidium* in this ripple trough. The *Tribrachidium* has evidently settled away from the trough axis of these oscillation ripples, where current would be faster than dead center in the trough; this may go against the filter feeding concept for this particular Ediacaran as it would presumably seek the quietest water considering that the food has to passively fall into pits according to the Rahman et al. (2015) hypothesis. A position in the trough slightly displaced from the trough midline might indicate orientation for photosymbiosis, in a configuration comparable to a tilted solar panel. The trough shape of a light colored substrate would even reflect more light to the *Tribrachidium*, indeed, some manufactured solar collectors have

Fig. 4.12 Mat stabilized ripples from Ediacara in South Australia with a *Tribrachidium* (*circled*) that had settled into the trough between the ripples. The impression is inverted as we are looking at the underside of a bed. The *Tribrachidium* has settled just to the right of the midline of the trough between oscillation ripple crests. Royal Ontario Museum specimen ROM 36218; ROM image used with permission. Lens cap 5.5 cm diameter

this shape and a similar function has been proposed for the dual trough shape of the enigmatic fern leaf shaped Ediacaran *Pteridinium* (McMenamin 1998). Finally, the position of the *Tribrachidium* in the sand ripple trough may have no special trophic meaning, but rather indicate that the *Tribrachidium* propagule was round like a single caviar egg, and rolled into the trough between the two ripple crests to occupy a relatively stable position by gravitational settling.

Figure 4.13 shows the result of the stabilized starved ripple phenomenon, with starved ripples overrun by microbial mat, again from the Proterozoic Clemente Formation in Sonora, México. In the close up image (Fig. 4.14), you can see the microbial mat forming elephant skin texture, and even nascent pustules, on the slip face (down current side) of the ripple. This may mean that the ripple slip faces were

Fig. 4.13 Starved ripples stabilized by microbial mat, again from the Proterozoic Clemente Formation in Sonora, México. Field sample 8 of 3/16/95. Scale bar in cm

Fig. 4.14 Starved ripples stabilized by microbial mat, again from the Proterozoic Clemente Formation in Sonora, México. Close up view of previous figure. Scale bar in cm

Fig. 4.15 Stabilized starved ripples, from a Mesozoic lacustrine locality at Mount Tom, Massachusetts. Scale bar in cm

oriented into the sun, thus encouraging rapid biomat growth (and consequent wrinkling) on the steeper lee face of the ripple.

Figure 4.15 shows the same phenomenon, stabilized starved ripples, from a Mesozoic lacustrine locality at Mount Tom, Hampshire County, Massachusetts. Although oriented in the other direction, the biomat stabilized starved ripples here look much the same as their Proterozoic marine counterparts. The mat wrinkles are even in the same place—the lee slip face (steep face) of the ripples—with the best wrinkle development slightly offset, perhaps indicating again the position of the sun and the vector of incoming solar radiation.

Treptichnid trace fossils are a paleontologically important ichnofossil group, because they have been formally invoked to define the Proterozoic Cambrian boundary. The trace fossil *Trichophycus pedum* (also known as *Phycodes pedum, Treptichnus pedum* or *Manykodes pedum*), one that often looks like a curving row of stitches, is characteristic for the earliest Cambrian rocks (Droser et al. 2002), although there is some evidence that its geological range extends a short stratigraphic distance beneath the formally defined ("golden spike") Proterozoic Cambrian boundary (Gehling et al. 2001). It represents a level of behavioral

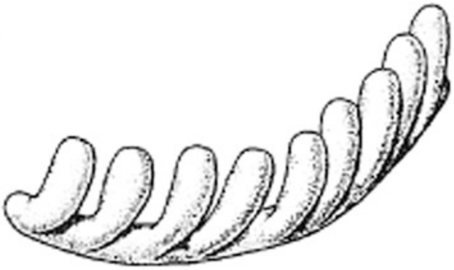


Fig. 4.16 *Trichophycus pedum*, an Early Cambrian and later ichnofossil formed by the sediment probing activity of a deposit feeding animal. Greatest dimension of ichnofossil 4 cm. Artwork by Dianna L. Schulte McMenamin

complexity that allows the presumably deposit feeding animal to form multiple probing tracks with significant vertical relief as it searches for food.

Figure 4.16 shows a sketch of earliest Cambrian *Trichophycus pedum*. Particularly nice examples of this ichnofossil occur in the Buen Formation of northern Greenland (Bryant and Pickerill 1990). The multiple upward curving branches of this burrow excavated by a deposit feeder may have left a pattern on the sea floor of curving tracks of holes if each branch punched through to the surface, and thus this treptichnid trace may be a precursor of the agrichnial (ectosymbiotic) graphoglyptid trace fossils that we will discuss in a forthcoming chapter.

Figure 4.17 shows a specimen of treptichnid trace *Treptichnus bifurcus* Miller, 1889 from the Gaulin Track site, Portland Formation, Holyoke, Massachusetts. It has the classic treptichnid 'row of stitches' appearance, in this case resembling the irregular stitches track made by a sewing apprentice. This particular specimen led to the first report of *T. bifurcus* from Hartford Basin strata (McMenamin 2005). It is an unquestioned treptichnid, and its occurrence with the other three features (size gradational mat pustules, tear drop structures, mat stabilize starved ripples) suggests that these four features constitute a suite or assemblage that represent a particular aquatic environmental type or state. That this same state reappeared in Mesozoic lakes, after having largely disappeared from the oceans 350 million years earlier, is telling us something important about the conjoined states of lithosphere and biosphere that together generate a particular lithosome, or body of sedimentary rock

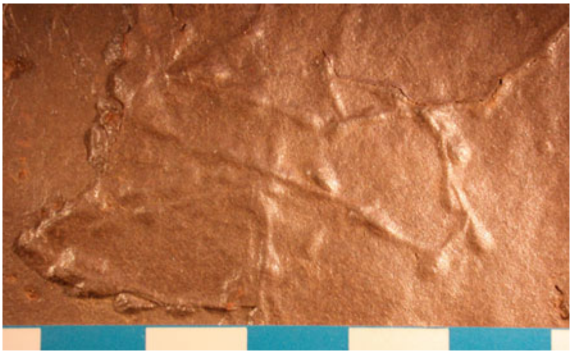


Fig. 4.17 Treptichnid trace *Treptichnus bifurcus* Miller, 1889 from the Gaulin Track site, Portland Formation, Holyoke, Massachusetts. Scale bar in cm

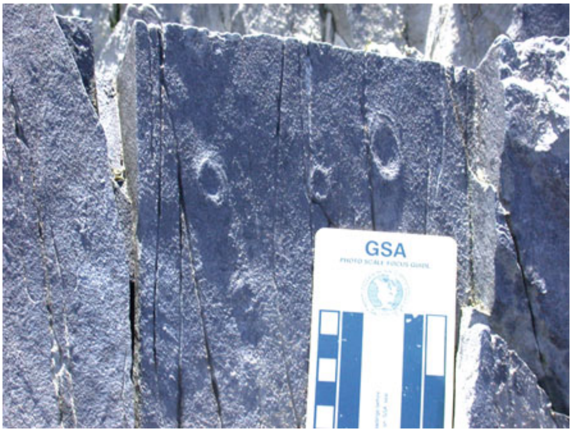


Fig. 4.18 *Aspidella* in outcrop occurring on the coast of Massachusetts near Hingham, Massachusetts in Late Proterozoic Cambridge Argillite. Scale bar (*left side* of scale) in cm

that is distinguished by particular sedimentary structures such as these. This then provides us with a very interesting example of environmental convergence.

It is important to emphasize that the treptichnid ichnofossils in the two analogous ecosystems, *Trichophycus pedum* and *Treptichnus bifurcus* respectively, were almost certainly not created by the same animal species, nor likely formed by the same type of animal. We do not know what the tracemakers were in either case (we will encounter a similar problem when we discuss graphoglyptids). We do know that very different types of organisms can create identical ichnofossils.

We may take this analysis one step further. *Aspidella* is the one of the simplest and also one of the most abundant types of Ediacaran fossils known. A rather wide variety of circular Ediacaran fossils have been synonymized into the genus *Aspidella* (Gehling et al. 2003). Figure 4.18 shows *Aspidella* in outcrop occurring on the coast of Massachusetts near Hingham, Massachusetts in Late Proterozoic Cambridge Argillite. The fossils consist of an elliptical raised structure with a central depressed area. Very curiously, there is yet another Massachusetts *Aspidella* locality. This one, however, is Mesozoic in age. The occurrence recalls Lyell's comment about *Iguanodon* reappearing in the woods. The fossil occurs in the Portland Formation lacustrine strata from Holyoke, Massachusetts.

Please be clear that I am not arguing that the Proterozoic *Aspidella* came back as a Lazarus taxon to inhabit Mesozoic rift basin lakes. Rather, although *Aspidella* does qualify as a body fossil rather than a trace fossil, the Mesozoic example most likely represents some type of holdfast impression, thus it represents the basal tip of a frondose organism that projected the upper part of its body into the water column for the purposes of photosymbiosis, osmotrophy, filter feeding or some mixotrophic combination of the above. The body plan of holdfast with frond is a winning strategy for aquatic organisms. It has arisen several times by convergent evolution in vastly different types of organisms, both solitary and colonial, ranging from seaweeds, to cnidarians such as sea pens, to bryozoans (fenestrate bryozoans such

Fig. 4.19 *Aspidella* in lacustrine shale. Arrow indicates position of elliptical structure with central cone interpreted here as a holdfast structure. Portland Formation, Arbor Way, Holyoke, Massachusetts, sample 6 of 7/1/2015. Scale bar in cm

as *Archimedes* raise this feeding strategy to a spiral art form), to frondose Ediacarans such as *Aspidella* and *Charniodiscus*.

Figure 4.19 shows the Mesozoic *Aspidella*. We see in this small fossil a circular depression with a central cone. I interpret this fossil as representing the holdfast of an Ediacaran grade, frondose organism of unknown affinity. It indicates the reappearance of the Ediacaran grade of organization in concert with the environmental convergence resulting from formation of the rift valley lake resulting from the breakup of Pangea, comparable to the way that the floor of the shallow sea in a Late Proterozoic rift ocean was formed by the breakup of Rodinia. The Mesozoic *Aspidella* is *likely* not a true (in terms of genetic affinity), freshwater Ediacaran from the Mesozoic (although this is not impossible); rather, it is probably a (presumably) multicellular creature of some sort that colonized the "simulated" Proterozoic conditions on the floor of a Jurassic lake. Lake conditions at the time were rather unusual, because the world had just gone through a harrowing double phased mass extinction (Permo Triassic and End Triassic) the worst double whammy on record.

The environmental convergences in these cases are rather striking. Three different biomat structures (that is to say, three variations on elephant skin texture), a treptichnid ichnofossil, and a distinctive yet enigmatic holdfast body fossil are common to both the Proterozoic and Mesozoic cases. This accounts for five separate features that are indicative for what might be called the Boundary Interval Biofilm Metazoan System State. This term is a bit cumbersome, but using the words "assemblage," "community," or "suite of guilds" would not be precise usage. We are discussing here a system state of part of the biosphere that attains a particular grade of organization and thus manifests a particular set of distinctive features, five to be exact. This system state is named for the Proterozoic Cambrian boundary interval because of distinctive markers of the Proterozoic (biofilms, Ediacarans) and the Cambrian Explosion (treptichnid ichnofossils). We can say not only that this represents a state of the system, but also that it may have characteristics of a metastable state, namely, one that is at or close to a phase shift in the overall behavior of the local or extended biosphere in question.

We may even be able to divide Earth history into three parts, typified by characteristic system states: Microbe World State (most of the Precambrian); Boundary Interval Biofilm Metazoan State, and post Cambrian Explosion State.

Interestingly, these states can manifest themselves in a somewhat time independent fashion. For example, lakes today can develop Microbe World State (consider the stromatolites growing today in Lake Fryxell, Antarctica; Young 1981) and Cambrian Explosion State (consider the many predatory freshwater amphipods; Dick 1995). Other states of lakes are possible as well. Consider Paul Olsen's analysis of the relationship between lake bottom bioturbation, preservation of laminae and organic matter influx (Olsen 1985). Olsen's scheme divides lakes into those with finely laminated bottom sediments, and those with homogenized sediments. The system state is influenced by the amount of available organic matter in the lake floor sediment. An excess leads to eutrophication; low amounts lead to an oligotrophic state. Those lakes that develop bottom sediments with well developed microlamination are either highly oligotrophic (and hence there is little food in the bottom sediment to attract burrowers) or highly eutrophic (large amounts of organic matter on the lake floor so deplete oxygen levels that burrowers cannot thrive). Lakes with intermediate levels of primary production (between about 0.25 and 0.5 $gC/m^2/day$) encourage benthic animals, whose burrowing activities homogenize the sediments.

The concept presented in this chapter may be generalized beyond Earth, as we can apply the principle of actualism ("The present is the key to the past") to other planets as well. The first convincing evidence for extraterrestrial life (assuming it is ever found) will consist of the actualistic recognition of two or more non symmetrical features 1, 2 or 3. Features 1–3 thus provide compelling search images for interplanetary fossil exploration. As an added benefit in this search, features 1-3 have wide ranges of potential occurrences in different aquatic depositional settings (i.e., lacustrine, oceanic, estuarine, etc.).

Searching for life on other planets is likely to involve challenges that go beyond mere recognition of Boundary Interval Biofilm Metazoan features 1–3. Exobiology explorers must ensure that they are focused on the proper scale to make the key observation. For example, I predict that any world that was able to host Microbe World global ocean biomats will at some point have developed giant stromatolites (Cloud et al. 1974) as well. Such structures from Proterozoic rocks of Canada, the Congo and California, up to 300 m in height (Bertrand Sarfati and Milandou 1989) and exposed by erosion of the overlying younger strata, are visible from space and arguably represent the largest fossils on Earth. If life exists today on, say, Mars, then it may exist in a subterranean biospheric system state that is alien to Earth or at least very unfamiliar to us.

Future geologists who explore the surface of planets will need to consider the fact that microbial mats can influence clastic sedimentation (and not just carbonate sedimentation, a process that seems largely restricted to Earth at this point). These biofilms can influence local depositional environments in characteristic and predictable ways. Non symmetry in the fossilized mat structures is key to actualistic recognition of their organo sedimentary nature.

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Chapter 5
Mat Farmers

Self-criticism, healthy doubt and curiosity are the guiding lights of innovation and new discoveries.
Boris Sergeevich Sokolov (1914–2013)

Abstract How old are the oldest animal trace fossils, and what size did they attain? Several candidate occurrences have been described. *Vermiforma antiqua*, *Plexus ricei* and the Trezona Formation structures are very ancient Proterozoic trace fossils. *Plexus ricei* occupied a now extinct 'mat–cutter' niche. The oldest biomat–associated ichnofossils occur in the Mina el Mesquite Formation (Cerro Las Bolas Group) near Sahuaripa, México. *Vaqueroichnus stewarti* n. ichnogen. n. isp. provides evidence for rudimentary microbial herding, the earliest hint of agrichnial activity in the trace fossil record. The oldest known tracemaker was about 4 mm long.

The origin of the earliest burrowing animals is a contentious subject in paleontology. A large part of the problem is mistaken identity: numerous pseudofossils have been published as the earliest known burrows. The quest for the first has engaged and ensnared some of the best minds in the paleontology business (Seilacher et al. 1998; Rasmussen et al. 2002; but see Jensen 2003). Even Ediacaran–age burrows and bioturbation (Rogov et al. 2012) have been subjected to controversy (Gámez Vintaned and Zhuravlev 2013; Rogov et al. 2013). Rolling balls of microbes, not animals, may have formed some early trackways (Matz et al. 2008). This is part of the phenomenon that Brasier (2010) referred to as the Mofaotyof ("My oldest fossils are older than your oldest fossils"; Green 2015) Principle. Even the most senior and experienced scientists can be tempted to publish the most ancient trace if the specimens seem to merit the attention. This effort is effectively paleontology's search for the ichnological Holy Grail. It is best to start discussion of the earliest trace fossils by listing the points on which the scientists involved in the research of these early ichnofossils all agree.

First, nearly everyone agrees that authentic ichnofossils, formed by animals, do in fact occur in strata deposited before the beginning of the Cambrian, although they are relatively rare. Second, many or most of these early trackways appear to have been formed by undermat miners, that is, animals that were burrowing

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underneath the surface of the ubiquitous Proterozoic microbial mats. The nutrient–rich scum that forms by partial decay on the underside of microbial mats might indeed be appetizing to a certain type of metazoan. The oldest reports of these undermat traces are called the 'Deep Proterozoic' records. There are a handful of accepted reports of this nature, ranging in age from 750–585 million years old. Much older reports, those, say greater than one billion or more years of age, have generally been discounted as misinterpreted sedimentary structures and/or pseudofossils.

Perhaps the most puzzling of the Deep Proterozoic trace fossils is called *Vermiforma antiqua*. Approximately 620 million years old, *Vermiforma* is known with confidence from only one site, although it may very well occur at other localities. The type slab preserves an enigmatic cluster of fossil structures from the Carolina Slate Belt. These were originally described as tubular worms (Cloud et al. 1976). At the time of their description, they were the oldest animal fossils known. Cloud and coauthor's vermiform fossils were later reinterpreted as ichnofossils rather than as the body fossils of ancient worms (Seilacher 2007).

The *Vermiforma* structures have an unusual property not seen in other fossils. Each one of the traces has the same complex shape as the ten other traces on the ancient bedding plane surface. No two tracks are identical, yet each seems to mirror a shared fundamental pattern. The pattern may be correlated from one track to the next. Cloud and coauthors had noted the common pattern, but it wasn't until the patterning was recognized as "quasiholographic" that the true strangeness of the traces became evident. The pattern of each trace has been described as a sequence of "a meat hook, a kink, and a pretzel" (Seilacher 2007).

Seilacher et al. (2000) presented a clever reinterpretation of *Vermiforma*, arguing that it actually represents a pseudofossil that Seilacher et al. (2000) called a "tectograph." In this view, pebbles rolling between two lithified beds of sediment formed the traces. As the beds slid past one another with a gyrating motion, back and forth along their shared bedding plane, the pebbles spun in approximate unison and inscribed the nearly similar tectograph patterns. In spite of the ingeniousness of the Seilacher et al. (2000) 'rolling rock' explanation, doubts were quickly raised about the validity of the tectograph model (Reed 2000; McMenamin 2001).

Hoping to get to the bottom of the controversy, in July 2000 I visited the *Vermiforma* slab at the Smithsonian. The slab has been broken up into approximately 14 pieces. The wooden pallet on which it sits is in poor condition, broken and with nails sticking out. The fresh rock is grayish green, classic Slate Belt volcaniclastic fine sediment. The upper surface bearing the *Vermiforma* specimens is weathered to a depth of approximately 0.5 mm. The color of the weathered rind is dark brown to limonitic tan. The *Vermiforma* traces are distinct but they do not seem to penetrate into the slab to any great extent.

The slab is approximately 20–23 cm thick. The lower 15 cm show obvious soft sediment slumping features. The upper 5 cm of the slab is intact stratification that is finely laminated. The top of the slab has, in addition to *Vermiforma*, elephant skin texture over much of its surface, indicative of preservation of a fossilized biofilm.

The key observation, however, is that there is another type of ichnofossil on the slab. Near a shallow core taken out of one side of the slab upper surface, a *Planolites*–like (or possibly *Helminthoidichnites*–like) trace fossil moves across the slab, and makes a distinct bend halfway through its track. In places, the *Planolites*–like ichnofossil has a distinctly undulose edge and in another place, it seems to develop a nodular or nodose aspect along its length (McMenamin 2001). The undulose track is 2–3 mm in diameter, and its shape is quite different from the congruent *Vermiforma* tracks.

With its elephant skin texture (also called Kinneyia structure; Porada et al. 2006), the surface of the *Vermiforma* slab represents an ancient microbially bound surface. Mat strength was sufficient to form a protective film that stabilized sediment even during times of high local water velocity. Metazoan burrows (the undulose burrow) lived in the immediate area, probably feeding beneath the mats as undermat miners.

The finely textured and well–preserved surface of this bed does not support a tectonic gliding or tectograph hypothesis. The surface is essentially intact and has not be smeared, scraped or otherwise tectonized. These observations falsify the tectograph hypothesis. The second type of ichnofossil has undulose edges, giving the impression that the animal was engaged in peristaltic burrowing or was even spiraling as it moved through sediment. The nodose zone on this trace gives a faint impression resembling beads on a string.

It seems safe to conclude that since *Vermiforma* occurs on a virtually pristine bedding plane surface, that the bed had not been tectonically altered. The *Vermiforma* specimens show layers of internal sediment packing (*spreite*, plural *spreiten*) that strongly resemble similar features in a trace fossil originally described as *Helminthoidichnites marinus* by Walcott (1898). A comparable spreite pattern occurs in a trace fossil attributed to *Zoophycos* isp. by Bryant and Pickerill (1990). Walcott (1898) called his *H. marinus* specimen the "cast of a boring in which the mud was pushed back by the animal that made it," and the same observation applies to *Vermiforma*. The *Vermiformas* occur with two other fossil types, the microbially induced sedimentary structure and the undulose track, and thus seems to be representative of a deep Proterozoic benthic animal community. The shared complex pattern of the ten *Vermiforma* specimens remains a fascinating question that is unexplained at present.

In a 2014 report that resonates with the strange case of *Vermiforma*, but curiously does not cite the *Vermiforma* work, Joel et al. (2014) announced the discovery of a new Ediacaran tubular organism assigned to the species *Plexus ricei*. The new fossil, from the Rawnsley Quartzite of South Australia, is presented as a tapeworm–like body fossil with bilateral symmetry. This interpretation of *Plexus ricei* is mistaken in almost exactly the same way that Cloud et al. (1976) erred in interpreting *Vermiforma antiqua* as a body fossil.

Plexus ricei forms a meandering loop on bedding planes that show some evidence for elephant skin texture. The trail is discontinuous, however, and this is apparently so because it represents the track of an animal that was burrowing underneath the microbial mat and cutting up through the mat, perforating it in places. The animal evidently had a sharp projection on its dorsal surface, something like the egg tooth in a chick, snake or turtle, or like a ‘rose spine’ on *Eokinorhynchus* (Fig. 1.15), that scored the biomat and left a narrow incised drag mark between places where the biomat was perforated as the burrowing animal moved along. Joel et al. (2014) argue, to the contrary, that (p. 260, italics or lack thereof, theirs):

> Plexus ricei *is not a trace fossil…. Plexus ricei* cannot be a trace fossil because, for a negative relief trace fossil to exist on the sole of a thick event bed, the trace fossil constructor first had to have mined down to that sedimentary layer.

In spite of the italicized phrase above, it is quite easy to see how *Plexus ricei* could form a negative impression on the sole of a bed if it was an undermat miner. The groove impression was simply formed under a biomat, which may have hardened in death mask fashion, thus forming the negative impression on the sole of the overlying event bed.

Apparent annulations in *Plexus ricei* are not like the segments in a tapeworm, but rather swellings in the punctured mat surface. Exactly why the *Plexus ricei* tracemaker was perforating the biomat in this fashion is not clear; perhaps it was providing for some ventilation underneath the surface of the biofilm. In any case, like *Vermiforma* before it, *Plexus ricei* is a trace fossil, not a body fossil. The annulations in *Plexus ricei* are comparable to the intermittent undulose edge of the *Planolites*–like trace fossil from the *Vermiforma* slab itself. *Plexus ricei* thus occupied a ‘mat–cutter’ niche that went extinct when widespread biomats ceased to form with the advent of abundant mat grazers, of which *Plexus ricei* itself may have served as the bellwether form.

The next section will introduce and describe the world’s oldest known animal ichnofossils. The trace fossils described here cannot have been formed by rolling microbial balls because they formed under microbial mats. They are not tectographs. The trackways are not quasiholographic. They cannot be the bodies of marine protists such as foraminifera or xenophyophores as they show the distinctive characteristics of directed motion.

The fossil discovery described here is from the Mina el Mesquite Formation of northwestern México, rocks dated to approximately 750–635 million years old (Corsetti et al. 2007). Interestingly, this age range matches both the age of the great Sturtian phase of Neoproterozoic glaciation (perhaps the worst single glaciation event in Earth history) and the breakup of the supercontinent Rodinia.

The Mina el Mesquite Formation occurs in the same part of the world (Sonora, México) that in 1995 produced the previously oldest, convincing ‘Deep Proterozoic’ trace fossils alongside very ancient Ediacarans (McMenamin and D’Ambrosio 1997). The fossils from the Mina el Mesquite Formation were found near the town of Sahuaripa, roughly due east of Hermosillo and hundreds of kilometers southeast of Caborca (Fig. 5.1).

The Mina el Mesquite Formation occurs in eastern Sonora as part of Cerro Las Bolas Group, a sequence of strata that includes, in stratigraphic order beginning at its base: a 20 m thick unit here named the Octavo Diamictite, the Mina el Mesquite

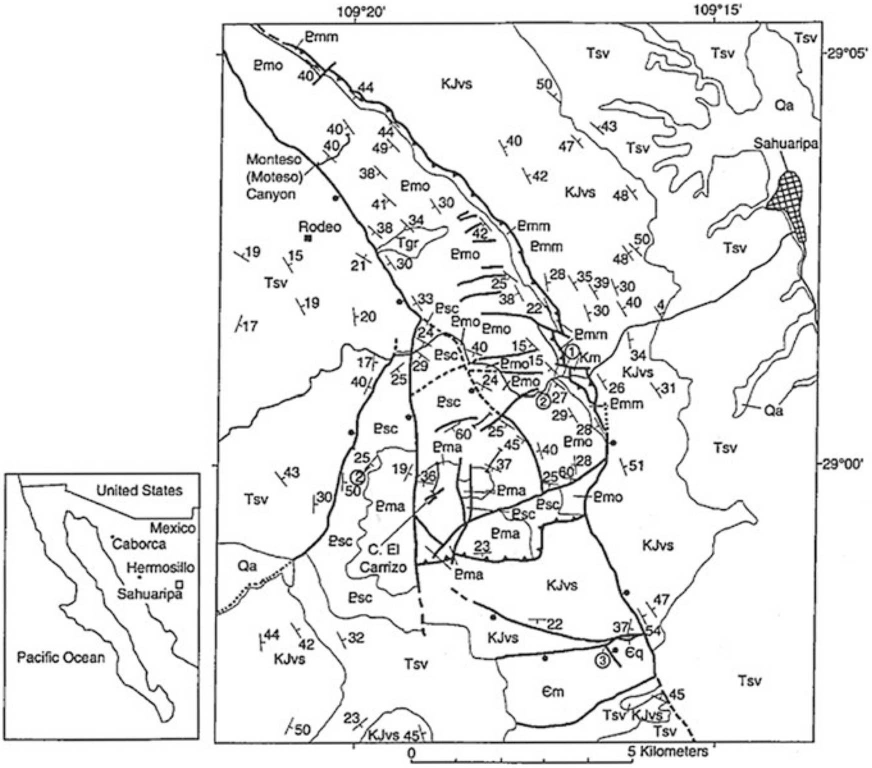
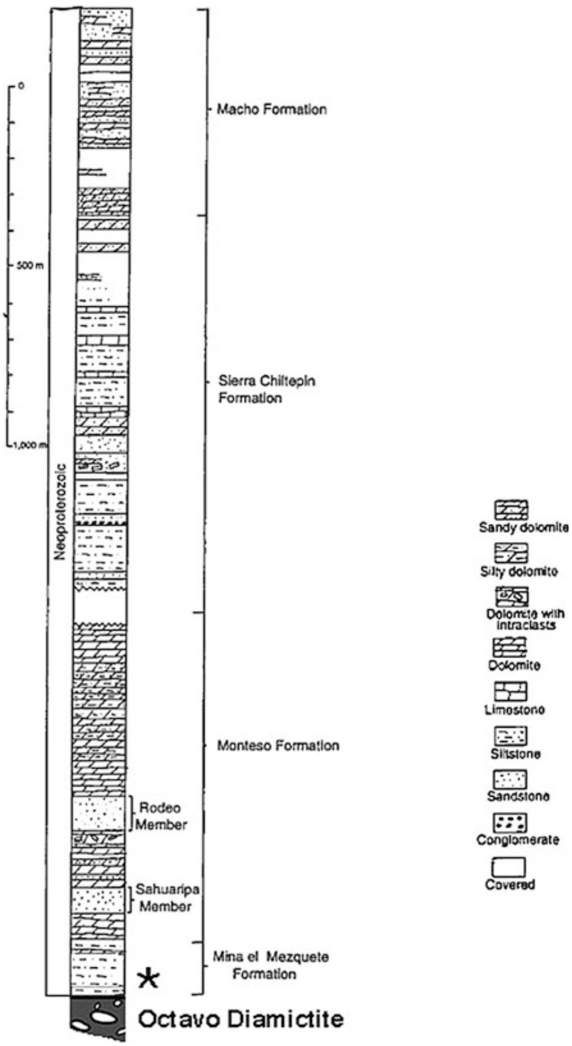


Fig. 5.1 Locality map for the fossils of the Mina el Mesquite Formation. Rock units as shown in explanation; fossil localities numbered as follows: 1, ichnofossils *Helminthoidichnites* isp. and *Vaqueroichnus stewarti* n. ichnogen. n. isp.; 2, stromatolites; 3, Middle Cambrian trilobite *Mexicella*. Explanation of map symbols: *Qa*, Quaternary alluvium; *Tsv*, Tertiary sedimentary and volcanic rocks, *Tgr*, Tertiary granitic rocks, *KJvs*, Cretaceous and/or Jurassic volcanic and volcanoclastic rocks; *Km*, Cretaceous siltstone and clayey to sandy limestone; *Cm*, Middle Cambrian strata, *Cq*, Lower and/or Middle Cambrian quartzite with *Skolithos* and other trace fossils; *Pmo*, Macho Formation; *Psc*, Sierra Chiltepín Formation; *Pmo*, Monteso Formation; *Pmm*, Mina el Mezquite Formation. Scale bar for main map 5 km. Geological mapping by John H. Stewart, United States Geological Survey

Formation, the Monteso Formation, the Sierra Chiltepín Formation, and the aptly named (because it is very resistant to erosion) Macho Formation at the top of the sequence. Figure 5.2 shows this stratigraphic sequence from the Octavo Diamictite to the top of the Macho Formation.

The Mina el Mesquite Formation is roughly 170 m thick, and consists of five separate units. The first (oldest unit), originally included in the Mina el Mesquite Formation, is in fact the Octavo Diamictite, and is excluded here from the Mina el Mesquite Formation. Corsetti et al. (2007) are unclear on this point, excluding the Octavo Tillite from the Mina el Mesquite Formation in the text of their article but including the tillite in the Mina el Mesquite Formation in their stratigraphic

Fig. 5.2 Stratigraphic section of the Cerro Las Bolas Group near Sahuaripa, México. *Asterisk* shows stratigraphic position of ichnofossils *Helminthoidichnites* isp. and *Vaqueroichnus stewarti* n. ichnogen. n. isp



columns. The Mina el Mesquite Formation thus consists of units 2–6 as originally numbered (Stewart et al. 2002). I will retain this unit numbering sequence for clarity's sake. Once again, unit 1 in this system is identical with the Octavo Diamictite.

Corsetti et al. (2007) assign the Octavo Diamictite to the Sturtian glacial epoch based on a dating technique that uses secular variation in stable carbon isotopes. Although less reliable than radiometric and other methods, and thus not foolproof, I endorse the Corsetti et al. (2007) correlation. The Mina el Mesquite Formation under this interpretation is somewhat younger than the Sturtian glaciation (750–700 million years). Corsetti et al. (2007) propose, and this also seems reasonable, that the Monteso Formation represents at least in part a cap carbonate deposit.

Glacial deposits in the late Proterozoic manifest a dyadic pattern that is often interpreted as representing the most extreme type (there were several such glaciations) of ‘whiplash’ climate change the world has ever experienced. This has caused concern among those worried about contemporary climate change; for the Proterozoic glacials show just how dangerously rapid climate change can occur and *has* occurred on the surface of Earth (Xiao 2004).

The characteristic pattern is a couplet. The lower half of the couplet is a deposit of a glacial origin known as a tillite (or if you are not absolutely certain that the rocks are glacial in origin, a diamictite). Tillites consist of angular, broken rocks of a variety of types set in fine–grained matrix. The usual interpretation of a tillite is that it represents the lithified version of mixed rocks and loose sediment (till) that, after having been transported for some distance mixed together with flowing glacier ice, was unceremoniously left behind by the melting glacier.

The upper half of the couplet is called the cap carbonate. Cap carbonates are typically composed of various mixtures of carbonate mineral types (especially dolomite, calcite and aragonite). Such minerals are not uncommonly encountered in ancient marine rocks (calcite is the main constituent of limestone, after all), but in cap carbonates the crystalline structure and composition of the rocks is very strange. Odd crystal fans projected upward from the sea floor, and dolomite was apparently precipitated directly from seawater, an otherwise very rare occurrence. The current interpretation of cap carbonates is that they represent a globally massive, largely non–biogenic carbonate mineral precipitation event on the Proterozoic sea floor in the immediate aftermath of the worst glaciation on record. Precipitation of this type is thought to require exceptionally warm ocean conditions. In most cases the cap carbonates are precipitated directly on top of the underlying tillite or diamictite, with the transition so sharp in many cases that you cannot fit a knife blade between the two layers (McMenamin 2004).

Thus we are confronted with the paradox of the three or perhaps four great pulses of late Proterozoic glaciation. The paradox is as follows. In each of these four pulses, the layer of rock formed during the extreme global cooling, the Snowball Earth layer, is immediately overlain by a layer of rock formed by extreme global warming. Hoffman et al. (1998) have called this the “freeze–fry” scenario. One might think that such extremes would come close to completely extinguishing life on Earth, or at least causing a major mass extinction. Ironically, the opposite seems to have occurred. The Ediacarans, the first complex life forms on Earth, appear suddenly (Shen et al. 2008) after the last Proterozoic ice age melts away.

These strange fluctuations in Proterozoic climate lead directly to the strangeness of the Mina el Mesquite Formation. Occurring as it does (Fig. 5.2; between the Octavo Diamictite [presumed to be a late Proterozoic glacial till]) and the Monteso Formation (presumed to be a cap carbonate), the Mina el Mesquite Formation occupies a unique place in the annals of stratigraphy. It is sandwiched between a Proterozoic till and a cap carbonate.

The Mina el Mesquite Formation represents a formation that should not exist and does not exist at the same stratigraphic horizon in most parts of the world. Apart from a few thin inter–tillite shaly layers in other stratigraphic sections dating to the subsequent (Marinoan) glacial epoch, there is little or no precedent for the Mina el Mesquite Formation. But it is there nevertheless. In terms of Earth history, the Mina el Mesquite Formation is the most important formation in the world because of its sandwiched stratigraphic position and because of the fact that it hosts the world's most ancient animal trace fossils.

The traces consist of a series of burrows associated with microbially–induced sedimentary textures (Fig. 5.3) and evidence for microbial mats in rock thin sections (Fig. 4.3) preserved in limestone probably from the Mina el Mesquite Formation units 5–6. These traces represent undermat burrows. Considering the age of the Mina el Mesquite Formation, with a nod to the Mofaotyof Principle, these represent the oldest convincing evidence for animal–grade complex life known anywhere in the universe. They are roughly 710 million years old, that is, they date to the end of the Sturtian interval of the Snowball Earth glaciations.

The bulk of the Sahuaripa samples consist of slabs of limestone up to 6 cm thick. The primary specimens consist of three part and counterpart pairs, and one representing a bed top without the corresponding overlying layers. The slabs were all originally labeled 6-F16-40J by United States Geological Survey geologist Jack Stewart. For clarity, I have added an additional label to Stewart's original labels using a letter in parentheses. The convention used for this as follows: (X) represents a bedding top, and (X′) represents bedding sole, or the underside of the overlying bed. Thus (X) and (X′) represent part and counterpart pairings.

The ichnofossils are visible on both the part and the counterpart. On the bed top (X), the tracks appear as shallow linear depressions. On the overlying sole (X′), the track casts stand out in relief and are thus called hyporeliefs. In this case, the details of the track pattern are clearer on the hyporelief than on the corresponding bedding top, although the trails are rather distinct in both cases. The specimens described here are labeled as follows: 6-F16-40J(A) [IGM 4724], 6-F16-40J(B) [IGM 4725], 6-F16-40J(B′) [IGM 4726], 6-F16-40J(C) [IGM 4727], 6-F16-40J(C′) [IGM 4728], 6-F16-40J(D) [IGM 4729], 6-F16-40J(D′) [IGM 4730] and 6-F16-40J(E) [IGM 4731]. 6-F16-40J(A) lacks its counterpart overlying sole, and the counterpart 6-F16-40J(D′) is more complete than part 6-F16-40J(D). The tracks in all specimens range from 0.7 to about 2 mm wide.

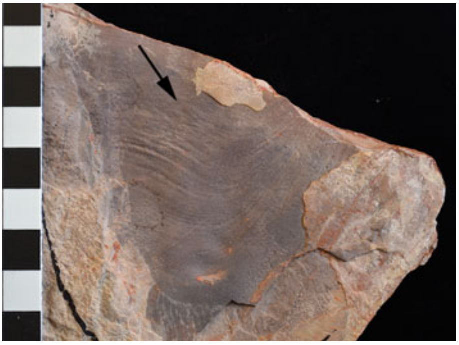


Fig. 5.3 Microbially–induced sedimentary structures in the Mina el Mesquite Formation, field sample 6-F16-40J(E) [IGM 4731]. The *parallel curving lines* on this bedding plane are formed by wrinkles in a biofilm. The *arrow* points to weakly developed mat pustules. Scale in cm

In sample 6-F16-40J(A) we see curving tracks that form open loops and Y–intersections in a few places (Fig. 5.4). The tracks are up to 2 mm wide, and seem to be somewhat larger than the tracks on the part–counterpart slabs. One of the track systems forms a closed, roughly needle eye–shaped loop 15 mm in greatest dimension.

In sample 6-F16-40J(B′), the slab is 37 cm in greatest dimension. The bedding plane surface is dominated by an undermat trackway that makes a curious closed rectangular loop (Fig. 5.5a), informally known as a "rubber band structure" and here named *Vaqueroichnus stewarti* n. ichnogen. n. isp. A second example of this ichnospecies is shown in Fig. 5.5b (slab 6-F16-40J[C′]). There are several other smaller tracks on the slab shown in Fig. 5.5a and its counterpart, including one that looks like a horizontal, serpentine sinusoidal burrow (Figs. 5.5c, d). This track is a variant of the zigzag track; it forms an open, roughly rectangular loop 4 cm in greatest dimension (Fig. 5.5c) plus a tiny closed loop as part of the trackway (Fig. 5.5d, arrow). The ichnofossil shown in Figs. 5.5c, d is referred to here as *Helminthoidichnites* isp.

In sample 6-F16-40J(C), the slab is 30 cm in greatest dimension. On this hyporelief surface we see a faint, long zigzag trace, a small roughly circular ring trace 8 mm in diameter (Fig. 5.6), several other short tracks, and a closed track that forms a roughly trapezoidal loop 7.5 cm in greatest dimension. As in 6-F16-40J(B′) (Fig. 5.5a), the bedding plane surface inside the closed loop (Fig. 5.5b) has a bumpy or reticulate texture that contrasts with the smoother texture of the bedding

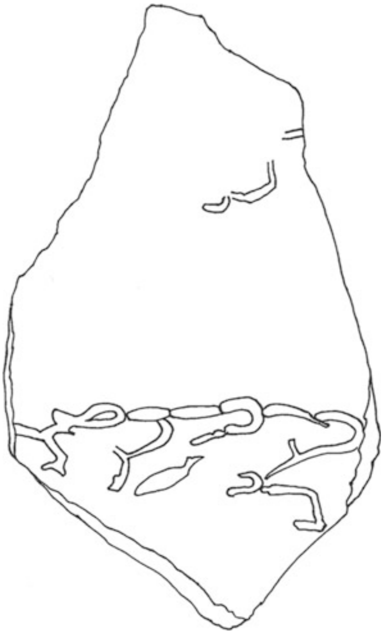


Fig. 5.4 Sketch map of unidentified ichnofossils forming curving tracks that form open loops and Y–intersections on sample 6-F16-40J(A) [IGM 4724], Mina el Mesquite Formation. Greatest dimension of slab 21.5 cm

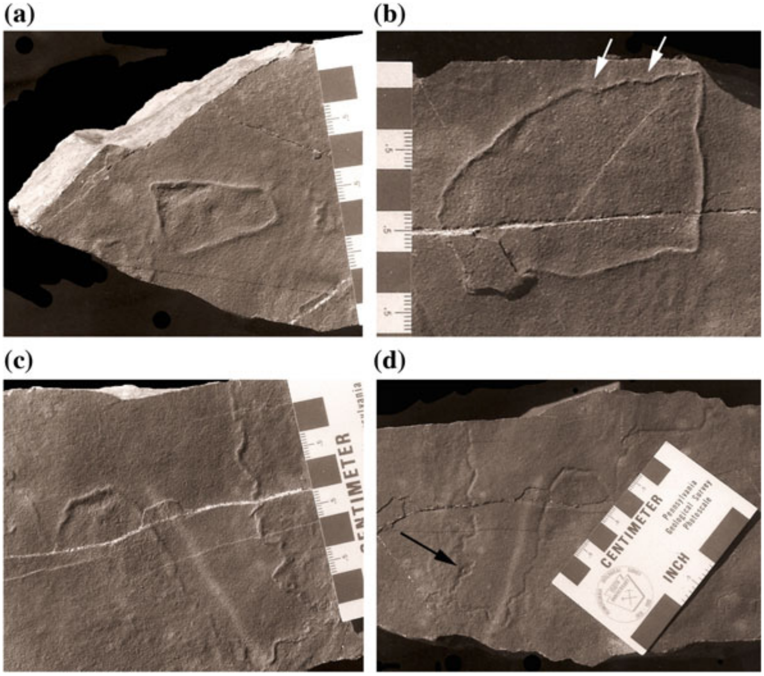


Fig. 5.5 *Vaqueroichnus stewarti* n. ichnogen. n. isp. “Rubber band structure” ichnofossils forming a curious rectangular loop undermat trackway: **a**, on slab 6-F16-40J(B′) [IGM 4726] note coarser biomat texture inside of the ichnofossil loop; **b**, on slab 6-F16-40J(C′) [IGM 4728]. The bedding plane surface inside the closed loop has a bumpy or reticulate texture that contrasts with the smoother texture of the bedding plane surfaces outside of the closed trapezoidal loop. This observation applies to both part and counterpart. *Arrows* show bends in upper edge of the track used to estimate the length of the tracemaker (see text). *Helminthoidichnites* isp., **c**, on slab 6-F16-40J(B′) [IGM 4726]; **d**, on slab 6-F16-40J(B) [IGM 4725], the counterpart, the *arrow* shows small loop formed by trackway. Scale bars in centimeters with millimeter fine scale

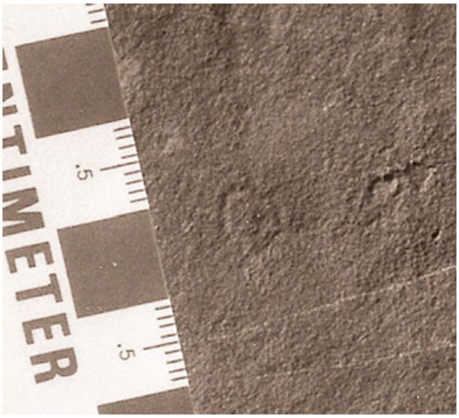


Fig. 5.6 *Vaqueroichnus stewarti* n. ichnogen. n. isp., Sahuaripa ring ichnofossil, sample 6-F16-40J(C) [IGM 4727]. Scale bar in centimeters with millimeter fine scale

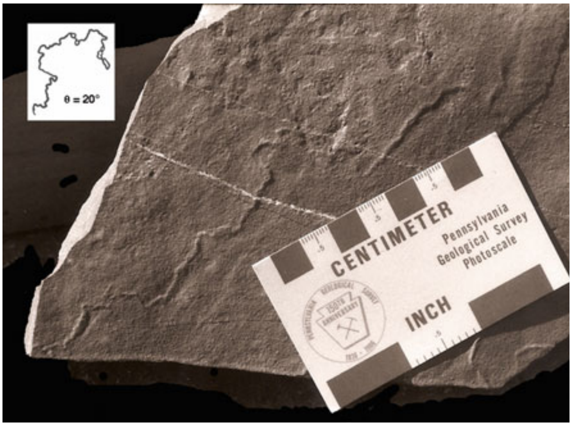


Fig. 5.7 *Helminthoidichnites* isp. Ichnofossil crosses nearly the entire length of the slab 6–F16-40J(D′) [IGM 4730]. Inset at *upper left* shows the tortuous track, redrawn from Hofmann's (1990) simulated trackway with θ = 20°. Scale bar in centimeters with millimeter fine scale

plane surfaces outside of the closed trapezoidal loop. This observation applies to both part and counterpart.

In sample 6-F16-40J(D′), the slab is 22.5 cm in greatest dimension. The most prominent feature is a zigzag track that crosses nearly the entire length of the slab, making roughly rectangular bends as seen in Fig. 5.7. Irregularly–spaced swellings occur along the length of this track. Another, incomplete track on this slab makes a hairpin turn, but does not appear to be part of a closed loop or corral loop structure.

These observations of the Mina el Mesquite Formation ichnofossils may be interpreted as follows. The tracks represent submat burrows formed by a small animal burrower, presumably some kind of bilaterian metazoan. The burrowing routine of this animal had three characteristics. Its foraging burrows show periodic sudden changes in direction (first order zigzags), with abrupt 90° and 120° changes in direction common. The overall trackway has large scale, rectangular bends. Relatively straight burrows, without the first order zigzags, close up to form closed roughly trapezoidal loops. The interior of these loops have a rougher texture (Fedonkin et al. 1994), and this texture represents a contained or *corralled* elephant skin texture biofilm, with enhanced growth of the microbial mat within the loop. The microbes in this case may have been farmed for food, but there is an alternate (and not mutually exclusive) additional explanation. It is possible that the metazoans were farming biomat microbes to increase available oxygen supplies beneath the biofilm. If so, *Vaqueroichnus stewarti* n. ichnogen. n. isp. served as oxygen respirators for these active, early tracemakers.

The Sahuaripa meander trail bears a striking resemblance to a computer–generated random pattern produced using only two variables—angular deviation per unit length and randomly determined turning directions (Hofmann 1990). Hofmann (1990) was able to generate simulated traces using the five parameters ϕ_0, S, θ, p and n, where ϕ_0 is the original direction of motion (as in "north–south," or in other words, $\phi_0 = 360°$), S is the length of the tracemaker, θ is an arbitrarily fixed angle of deviation ($= d\phi/S$), p is probability ($p = 0.5$) that the animal will turn to the left or the right, and n is the next number in a sequence of random numbers used to determine whether or not the turn is to the left or to the right.

The meander trace fossils compare most closely to the simulated trace fossil shown in Hofmann's (1990) Fig. 2B, in which there is a deviation of 20° per advance increment (Fig. 5.7). Increasing this angle of deviation (θ) results in what Hofmann (1990) calls "an increasingly tortuous aspect" of the simulated ichnofossil. Thus, the simulated trace of $\theta = 20°$ is intermediate in tortuosity between simulated traces with values of θ between 10° and 30°.

A value of 20° generates a track that is neither too much like a straight path (as is the case for 10°) nor too convoluted to cover very much distance across the bedding plane surface (as is the case for 30°), and thus may represent a biologically useful "compromise setting" for a burrowing behavior governed by a simple set of rules (Figs. 5.7 and 5.8). This setting may be an optimal solution in this system to the problem of efficiently locating food sources on a bedding plane surface. This implies that higher quality food resources underneath the biomat were not uniformly distributed. (Fig. 5.8)

The resemblance between the Sahuaripa traces and Hofmann's (1990) computer simulations is striking, even to details of the morphology of the track, such as small loops formed when the track doubled back on itself (Figs. 5.5d and 5.7). Detailed comparisons of the fossils show that they have a tortuosity intermediate between simulations with θ values between 15° and 20°, with an average value for the actual fossils of approximately 17°. These results strongly suggest that Hofmann's (1990) analysis successfully unveiled rules that do indeed describe the developmental geometry of actual trace fossils, at least when applied to the earliest known traces.

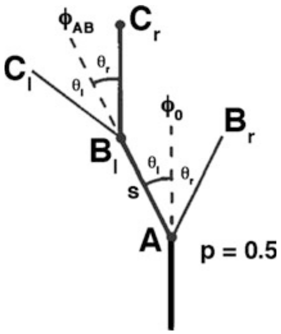


Fig. 5.8 Simulated ichnofossil shape parameters. A–B_l–C_r. represents the ichnofossil path. The *thick line* shows the actual path chosen, and the *thin lines* are alternate routes not followed. The deviation direction, with equal probability (p = 0.5) for a *left* (${}_l$) or *right* (${}_r$) turn, is selected at random. Headings (or azimuth, ϕ°) are shown by *dashed lines*. S equals the unit distance of advance, and also represents the length of the simulated animal tracemaker. According to Hofmann (1990): "$\theta = d\phi/S$ = the size and direction of the turning angle (deviation) per S–unit from previous heading (positive to the *right* [θ_r], negative to the *left* [θ_l]). The overall orientation of the trace A–C_r is governed by the initial heading, here set arbitrarily to $\phi_0 = 360°$." Diagram modified from Hofmann (1990)

The angular, closed loop tracks ("rubber band structures") are considered here to have been formed by the same tracemakers that formed the tortuous meander trace, only in this case the tracemakers were following a different behavioral program or routine. Not counting the angular bends required to close the loop, the θ value for these traces is much lower, matching closely the shape of the 2.5° tracks in Hofmann's (1990) simulation.

The Sahuaripa trace maker thus demonstrates what appears at first glance to be a fairly sophisticated behavioral repertoire, but which in fact merely represents two alternating modes of trace making distinguished by a simple variation in the value of θ. Mode 1 forms the meander track (*Helminthoidichnites* isp.) and is characterized by θ = 17°. Mode 2 forms the corral burrow (*Vaqueroichnus stewarti* n. ichnogen. n. isp.) and is characterized by θ = 2.5° combined with three sharp bends to close the loop. The behavioral program and feeding strategy implied by this trace fossil have a decidedly unsophisticated or "primitive" aspect, as would be expected for a trace fossil formed so close to the presumed origin of Metazoa.

The comparison between the Sahuaripa traces and Hofmann's (1990) simulations is sufficiently close that the length of the tracemaker may be estimated with some confidence from the rubber band track shown in Fig. 5.5b. This specimen of *Vaqueroichnus stewarti* n. ichnogen. n. isp. shows two gentle bends in the track along its upper edge in Fig. 5.5b (arrows). The two bends are virtually identical to the single bend shown in Hofmann's (1990) simulation with the setting θ = 2.5°. This observation in fact provides the basis for assigning a value of θ = 2.5° to the corral ichnofossil. Assuming that the opposite end of each bend represents a single body length of the burrowing animal (as seems reasonable after inspection of Fig. 1 in Hofmann 1990), the body length of the animal measures S = 4 mm. This is a very useful result as it provides body size estimate (approximately 1.5 mm by 4 mm) for the earliest known Proterozoic burrower.

The Mina el Mesquite burrower had both a deposit feeding/foraging capability (as shown by the first order and second order zigzags of the foraging traces), plus an agrichnial capability. The closed loops, with relatively straight burrow edges (no zigzagging required), represent an alternate behavior of the animal that is suited to creating microbial biomat farms. These are referred to here as 'corral structures'. The animal somehow enhanced the growth of the biofilm within the confines of the corral structure, and this is why its interior surface texture is rougher. There is better–developed elephant skin texture inside of the corral structure because the biomat grew better there, presumably thanks to tending and possibly fertilizing by the farmer metazoan.

The results here suggest that agrichnial ichnofossils, that is, trace fossils showing evidence for metazoan farming of microbes, represent a very early, and perhaps *the* original type of trace fossil. The fact that micro–elephant skin texture is concentrated within the closed corral structures strongly suggests that early burrowing metazoans were not only interacting with the microbes that formed their overmat ceiling, but were *also* actively managing and farming them to increase food supplies by making the fairly easily constructed *Vaqueroichnus stewarti* n. ichnogen. n. isp. trace fossil. Thus agriculture, as shown by these earliest, agrichnial ichnofossils, appears as old as metazoans themselves at least as far back as we can see in the fossil record. Suggestions that presumably agrichnial graphoglyptids such as *Protopaleodictyon* evolved from non–graphoglyptids such as *Multina* may very well be correct (Zapata et al. 2016), but should be seen as an atavism if indeed the earliest trace fossils were agrichnial. In other words, agrichnical farming may have preceded foraging.

The Trezona Formation of Australia hosts an ancient (640–650 million years; pre–Marinoan glaciation) “heiroglyphic limestone” that has puzzled researchers for decades (Collinson and McMenamin 1984). They have been described as desiccation features and even putative sponges (Maloof et al. 2010), but are in fact mineralized, naturally excavated, and remobilized burrows. A better candidate for earliest sponge, complete with a network of pores distributed over its surface, is *Blastulospongia* (Conway Morris and Menge 1990).

The morphology a burrow lined by a mineralized layer is shown in Fig. 5.9, an image of an Early Cambrian fossilized burrow from the Puerto Blanco Formation. This ichnofossil has bulges along its length rather than being evenly cylindrical. The burrow lining was replaced by silica and then removed from the rock by means of acetic acid dissolution. The Trezona Formation structures are similar, although they were naturally removed from soft sediment by current winnowing and reworking after they had become lithified in advance of the lithification of their initial limey matrix. The Y-, T- and undulating tube shapes of the structures (Figs. 5.10 and 5.11)

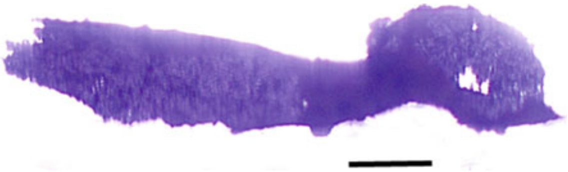


Fig. 5.9 Photomicrograph of fossilized burrow from the Lower Cambrian Puerto Blanco Formation (unit 2), Sonora, México, field sample 6.5 of 12/17/82. This specimen co–occurs in unit 2 with *Palmettaspis* sp. (= cf. *Fallotaspis* sp. of McMenamin (1987), currently the oldest known trilobite in México, W.H. Fritz, written communication, July 23, 1997; IGM 3652). Scale bar = 1 mm

Fig. 5.10 Erosion–mobilized Y-shaped burrow, Proterozoic Trezona Formation, South Australia. Slide PCH-1. Scale in mm

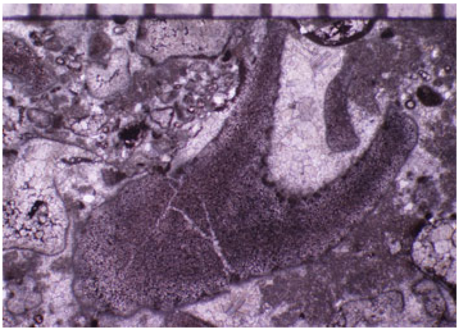
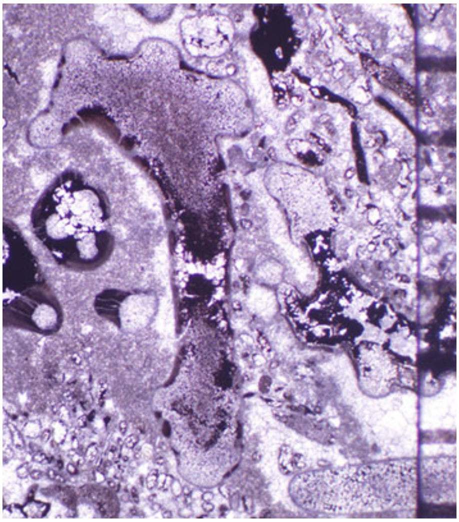


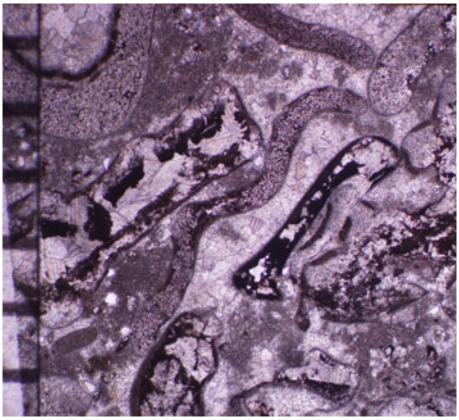
Fig. 5.11 Erosion–mobilized T-shaped burrow, Trezona Formation, South Australia. Herniations in the burrow walls may be the result of microbially–derived gas inflation of the burrow. Slide PCH-5. Scale in mm



can at last be correctly interpreted as mineralized burrows that were excavated by currents and redeposited. One erosion–mobilized burrow (Fig. 5.12) has a shape that is identical to commonly seen, curved cylindrical burrows.

Several of the erosion–mobilized burrows show laminated internal linings to the burrow wall (Figs. 5.13 and 5.14, lower left); in fact this seems to constitute part of the burrow wall and probably helped to harden the burrow tube and render it capable of surviving transport. This constitutes strong evidence favoring an agrichnial function for the trace fossils. The microbial burrow linings were growing so well inside the tube that they laid down successive layers of mineralized tubular biomats. It is as if a stromatolite had been turned inside out and rolled into a cylinder. And as if in a hearty tribute to elephant skin texture, one of the erosion–mobilized burrows has the shape of an elephant's trunk (Fig. 5.14).

Fig. 5.12 Serpentine–sinusoidal erosion–mobilized burrow, Slide PCH-11. Trezona Formation, South Australia. Scale in mm



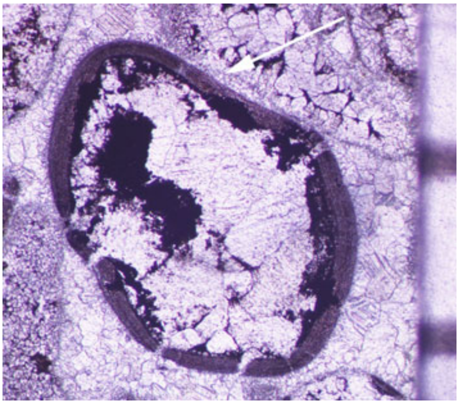


Fig. 5.13 Erosion–mobilized burrow seen in cross–section, showing laminated internal linings to the burrow wall. The slightly crinkly nature of these laminations (*arrow*) indicates that they represent successive microbial biofilm layers/accretions to the interior of the burrow. Note that the microbial lamination–reinforced burrow wall is cracked in a number of places. Trezona Formation, South Australia, Slide PCH-11. Scale in mm

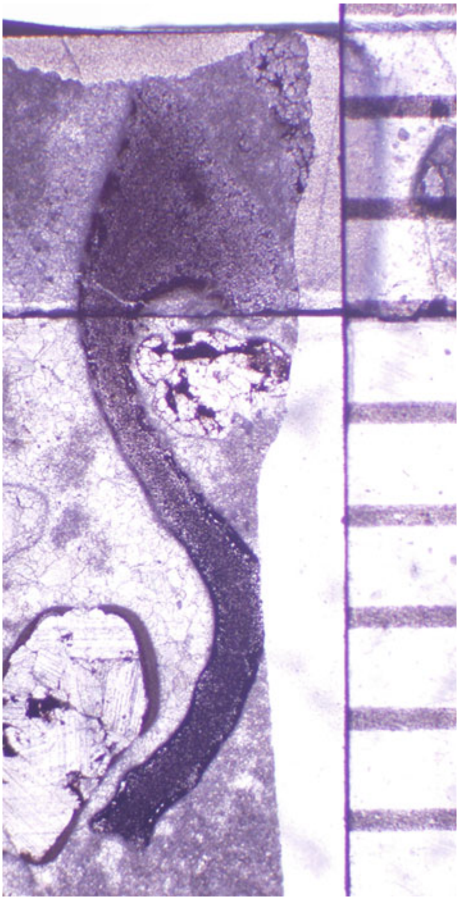


Fig. 5.14 Erosion–mobilized burrows with shape of an elephant's trunk [slide PCH-3], Trezona Formation, South Australia, Slide PCH-3. Scale in mm

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Chapter 6
Etch Stop

> *Rolling stones gather no moss.*
>
> Titus Livius (Maxim 524)

Abstract Why does the Proterozoic shelly fossil *Qinella* occur in a Cambrian limestone? *Qinella's* unique shell morphology, thin walls separated by fluid–filled spaces (etch stop defense), served as an effective deterrent to Cambrian shell–boring predators. Family Cloudinidae was likely driven to extinction by first boring, and later crushing, predators. *Qinella* provides an excellent example of the predator–prey escalation that took place during the Early Cambrian.

The Ediacaran Biota remains largely mysterious and is as controversial as ever. Even the phrase 'Ediacaran biota' is contentious. MacGabhann (2014) credits me with coining the phrase (McMenamin 1982), and then argues in his provocative article that 'biota' is a misnomer because it implies that the Ediacarans can be treated as a single coherent group. While acknowledging MacGabhann's point that the Ediacarans surely do represent multiple lineages of different types of organisms, I think that it is evident that with the Ediacarans we have a group of creatures that can indeed be treated as a unified whole because of the peculiar paleoecology of their Proterozoic world. Uncertainties abound regarding the nature of this ancient aquatic biosphere. Certain aspects, however, of Ediacaran World are coming into clearer focus. There does seem to be an emerging consensus that many of the Ediacarans were osmotrophs (McMenamin 1993). Photoautotrophy and chemoautotrophy are also likely to have been utilized by Ediacarans.

The unornamented, upright Ediacaran fossil *Funisia dorothea* resembles fat fingers sticking up from the sea floor consisting of many stacked, rounded segments. *Funisia* is said to have reproduced sexually because of its occurrence in large cohorts, each presumably representing a single spatfall (Droser and Gehling 2008). However, its morphology of stacked metacells suggests that a metacellular (McMenamin 1998), and possibly asexual, lifestyle is more likely. One can easily imagine synchronized budding of the terminal metacell in a group of *Funisias* set to launch the next generation. Indeed, this is very much the reproductive mode advocated for metacellular Ediacarans.

M.A.S. McMenamin, *Dynamic Paleontology*,
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Funisia occurs in the Ediacara strata of South Australia, without doubt a photic zone habitat. With no other apparent means of acquiring nutrition, *Funisias* were most likely photosynthetic or photosymbiotic. *Funisia* individuals occur in such dense stands that osmotrophic feeding would be seriously impaired, and they lack the filtering apparatus that is the usual requirement for filter feeding. During reproduction, each propagule metacell under the photosymbiotic interpretation would carry its own supply of internal photosymbionts. In this small neat round propagule package, the two symbionts (host and photomicrobe) would go off to establish a new *Funisia* garden.

A looming problem remains regarding the question of the feeding strategy of putative deep water Ediacarans of the Avalonian biota. These represent the "second wave" of the Ediacaran evolutionary radiation (579–565 million years ago; Shen et al. 2008), following the appearance of the oldest Ediacaran communities in shallow water in Sonora, México (585 million years ago; McMenamin 1996).

If the Avalon creatures lived well beneath the photic zone, then why were some of them so tall, reaching beyond 2 m as if they were straining upward to capture faint light emanating from shallower waters? The artistic reconstructions of frondose Ediacarans such as *Charniodiscus* and *Charnia* typically fall into one of two categories. In type one, the fronds are a lively green, often variegated, and sway beautifully above the Proterozoic sea floor. In type two, the fronds are washed–out and deathly pale, living in a lightless world illuminated only by the imaginary flood lamps of a time–travelling submersible.

In an attempt to address the problem of Ediacaran food acquisition, Ghisalberti et al. (2014) made a case for aphotic osmotrophy in the Avalonian Ediacarans. They wrote:

> We reconstructed flow–velocity profiles and vertical mixing using canopy flow models appropriate to the densities of the observed communities. Further modeling of processes at organismal surfaces documents increasing uptake with height in the community as a function of thinning of the diffusive boundary layer with increased velocity… In benthic communities of osmotrophs of sufficient density, access to flow in low–flow settings provides an advantage to taller architecture, providing a selectional driver for communities of tall eukaryotes in contexts where phototropism cannot contribute to upward growth (p. 305).

There are several methodological difficulties associated with the claims presented in this paper. First, Ghisalberti et al. (2014) make the assumption that phototropism cannot contribute to upward growth. This is not necessarily the case, as amount of illumination (from sunlight, bioluminescence, etc.) reaching the Proterozoic Avalonian sea floor is unknown, and assumptions that these Ediacarans lived in absolutely pitch-black darkness are unwarranted. We simply do not know how bright conditions were on the Proterozoic sea floor, regardless of whether we are speaking of a deep marine or shallow marine habitat. As Lynn Margulis once put it, if one photon reaches the sea floor, there will be an organism there to capture it.

Second, the authors make an argument based on conventional natural selection (as in, "selection driver") that assumes that the large Ediacarans were in direct competition with sea floor, biomat–forming microbes. This erroneous idea is driven by an obsolete Darwinian notion of individualism that ignores potential synergistic interactions between the creatures of the Proterozoic seas, such as the fact that algal users of glycolate dehydrogenase are forced to excrete larger amount as unmetabolized glycolate (an osmotrophy nutrient) into seawater during times of increased oxygenation of the water (McMenamin 1993). The paper also ignores the fact that many of the Ediacarans on the Avalonian times seafloor were flat and prostrate, such as the spindle–shaped *Fractofusus*. These spindles are among the more common in the Avalonian biota. Indeed, osmotrophy may have worked better directly on the sea floor, juxtaposed against the sources of organic matter that released the nutrients in the first place. Benthic microbial osmotrophs of biomats thrive in this position on the sea floor.

The authors' press release lists the Avalon Ediacarans as only reaching 1 m in height ("These enigmatic leaf–shaped life forms reached up to a meter in height"), whereas the actual height is more than 2 ms (*Charnia wardi*; Narbonne and Gehling 2003). The misstatement deflects attention away from the fact that a 2 m frond is not gaining significant additional nutrients from osmotrophy by being so tall, whereas it could very well be gaining more exposure to light. The authors' (their Fig. 4B) curve plotting height (cm) versus increase in uptake (per unit of surface area per unit of concentration, in cm/s), goes approximately flat (Fig. 6.1) at approximately 15 cm, with minimal further osmotrophic gain with increased height from the substrate. To make this a bit clearer, I have redrafted their figure as shown in Fig. 6.1. Note how the curves flatten out at 15 cm. The height advantage for osmotrophy by being 15 cm tall is negated by the likely higher concentrations of nutrients nearer their source on the organic–rich sea floor. The authors' knee–jerk reaction against the green frond reconstruction has skewed the science in an attempt to sway scientific opinion against the concept of photosymbiosis in Ediacarans.

In summary, much remains to be learned about Proterozoic paleoecology and the paleobathymetry of the creatures that formed these communities. Passions run high on these issues. This tension is good for science as it keeps scientists honest and focuses attention on the most important topics. Let's now consider the paleoecology of the Cambrian, and in particular the paleoecology of the Cambrian Explosion interval, where predatory heterotrophy suddenly asserts itself on the sea floor on a scale that overwhelms the osmotrophy, photosymbiosis and chemoautotrophy of Ediacaran times.

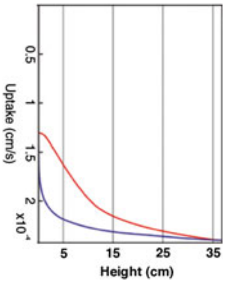

Fig. 6.1 Ediacaran frond nutrient uptake as a function of height off the *bottom*. The bivariate plot shows increase in uptake (per unit surface area per unit of concentration, cm/s) with height above the *bottom*. Redrafted from Ghisalberti et al. (2014)

Fig. 6.2 Ordovician trilobite *Asaphus emoryi* Hall 1859. This asaphid trilobite was collected from near El Paso, Texas during the 1850s Emory expedition. It was the first trilobite fossil reported west of the Mississippi River. USNM 9824; scale bar in cm. Courtesy of Smithsonian Institution. Photograph by M. McMenamin

Interestingly, the earliest shelly animal fossils appear not during the Cambrian Explosion itself, but in the late Proterozoic. These animals were contemporaries of the Ediacaran soft–bodied fossils, although the two types are typically found in different depositional settings. The cloudinids and sinotubulitids have tubular skeletons with walls that show a multilamellate structure.

Ever since the 1859 discovery of the early Paleozoic trilobite *Asaphus emoryi* (Fig. 6.2), collected in the 1850s by the Emory expedition that explored the southwestern regions of the United States, southwestern North America has provided a series of important localities and specimens that have played a major role in attempts to understand the puzzling dynamics of the Cambrian Explosion. Attempts to better understand the nature of the Cambrian boundary transition were significantly advanced by a serendipitous fossil discovery made during a Mount Holyoke College field expedition to Death Valley, California in March 2012.

During a Spring Break field trip to Death Valley (the Death Valley Field Course; Fig. 6.3), ten samples of weathered carbonate rock were collected from the second of four desert pavement surfaces developed on a wind–swept alluvial terrace near the mouth of Echo Canyon, Death Valley, California (Sharp and Glazner 1997). Our field party was originally intending to search for evidence of the Ediacaran biota in the upper reaches of Echo Canyon, but vehicular problems with our rental vehicle forced us to stay closer to the main road and hence, closer to the mouth of Echo Canyon.

This mishap led to an important discovery. The stepped series of terraces form an interesting geomorphic feature that we informally called the “Bear Claw Plateau” (so named due to its shape as seen from the air; Figs. 6.4 and 6.5). Our

Fig. 6.3 Students C. Sharma, J.M. McMenamin and W.A. Hughes are frozen in mock terror as they examine giant clasts in Mosaic Canyon, Death Valley, California. *Photo credit* P. Taylor

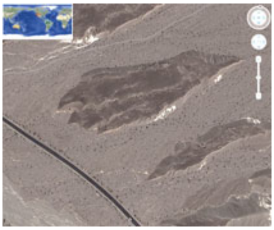

Fig. 6.4 Google Earth image of the Bear Claw Plateau. The *white spots* on its southeastern edge are outcrops of the Furnace Creek Formation. Note vehicle for scale on south end of road

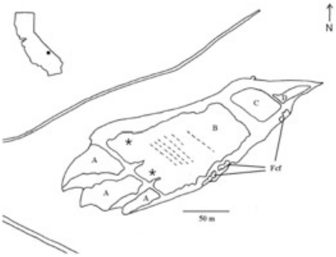

Fig. 6.5 Geological map of the Bear Claw Plateau, showing the extent of desert pavement terraces. *Inset map* shows location of site. *A*, *B*, *C* and *D* are successively higher terraces on the plateau. *Fcf*, outcrops of the Furnace Creek Formation. The road to the northwest is Echo Canyon Road, the road to the southwest is Interstate Highway 190. *Asterisks* show the position of desert pavement limestone samples 2 of 3/21/2012 (northern locality) and 6 of 3/21/2012 (southern locality). Geological mapping by M.A.S. McMenamin, W.A. Hughes and J.M. McMenamin

geological map of the site (Fig. 6.5) suggests that the core of the Bear Claw Plateau consists of resistant outcrops of the 3–5 million year old Furnace Creek Formation. These relatively resistant outcrops of Furnace Creek Formation evidently protected the plateau from being completely obliterated by sheet flood erosion on all sides. A curiously displaced block of even older fanglomerate (i.e., a conglomerate formed by an alluvial fan), reminiscent of the famous embedded blocks at Mosaic Canyon in Death Valley, adheres to the north side of Bear Claw Plateau. Curiously, the fossiliferous rock samples were found only on Terrace 2, and did not occur on the other desert pavement terrace surfaces.

The fossiliferous rock samples, collected under a National Park Service collecting permit, were oolitic and were weathered to a buff tan color. Our initial thoughts were that the rock samples might be derived from Proterozoic strata. The weathered color and oolitic character of the carbonates suggested a possible comparison with the Proterozoic Rainstorm Member of the Johnnie Oolite (Johnnie Formation) that is known to crop out in the vicinity of Echo Canyon. Furthermore, fossil specimens strongly resembling cloudinid fossils were visible on weathered surfaces of the rock, seemingly in accord with our field inference that the carbonates might be of Precambrian age.

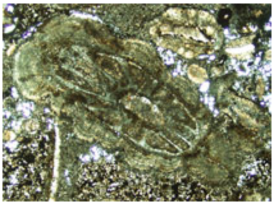

Fig. 6.6 *Ethmophyllum*-type archaeocyath from the Bear Claw Plateau. The ethmophylloid archaeocyath is seen in an oblique transverse section, with the central cavity showing as a central ellipse. Note the prominent cerebroid (resembling the brain or cerebrum) coating of the fossil, and also the large pores in the inner wall carcass of the archaeocyath. Wood Canyon Formation, lower oolite, Lower Cambrian, field sample 2 of 3/21/2012. Greatest length of oblique section through fossil 4 mm. Notwithstanding the undoubted Cambrian age of the rock, the thin sections and fossils exposed on weathered surfaces showed the presence of tubular shelly fossils belonging to the Proterozoic genus *Qinella* (Figs. 6.7 and 6.8)

Laboratory analysis and thin–sectioning back at the Paleontology Laboratory at Mount Holyoke, however, indicated that the rock samples were not dolostones from the Johnnie Formation, but rather Cambrian limestones. We were able to determine this due to the presence of both archaeocyaths and trilobite shell fragments (McMenamin et al. 2013). One thin section sliced obliquely through a relatively intact specimen of a small archaeocyath of the *Ethmophyllum* type, so identified because of the huge pores still visible in the inner wall (Fig. 6.6). The ethmophylloid archaeocyath is encrusted with a cerebroid layer of calcium carbonate, as are the ooids and other coated grains in the sample. Cerebroid grain coatings are characteristic for the lower oolite of the upper Wood Canyon Formation (Corsetti et al. 2006), a Cambrian formation of the Death Valley region that is known to contain archaeocyaths.

Qinella is a member of a group of mostly Proterozoic organisms known as cloudinids, and is assigned here to Family Cloudinidae. These creatures formed one of the earliest known mineralized skeleton types consisting of lightly mineralized tubular skeletons consisting of multiple walls. Cloudinids probably represent some type of worm–like metazoan. Arguments that cloudinids are "sponge–like" (Cohen 2006) may be rejected because their skeletons are not porous and thus they would not be able to filter feed in the sponge or archaeocyath manner.

The genus has eccentrically tube–in–tube walls (Figs. 6.9 and 6.10). *Cloudina* differs from *Qinella* by having more steeply sloping internal walls, and *Qinella* differs from *Sinotubulites* by having greater spacing between wall laminae for the length of the tube. In the Death Valley *Qinella*, tapering contacts are visible between adjacent walls as seen in thin section (Fig. 6.9) and via cathodoluminescence (Fig. 6.10).

Arguments that the range of cloudinids (McMenamin 1987) extended into the Cambrian were questioned by Grant (1990) who argued that all these fossils should be assigned to the genus *Cloudina*, and that they thereby could be used as index fossils for Precambrian strata. Both inferences proved to be incorrect. *Cloudina* and

Fig. 6.7 *Qinella* occurring in a float sample of the Bear Claw Plateau, mouth of Echo Canyon, Death Valley. Tubes are exposed on weathered rock surface. Alluvial terrace #2, Wood Canyon Formation, lower oolite, Lower Cambrian, field sample 2 of 3/21/2012. Scale bar in cm

Fig. 6.8 *Qinella* from float samples of the Bear Claw Plateau. Detail of fossil exposed on weathered rock surface. Maximum width of tube 3 mm

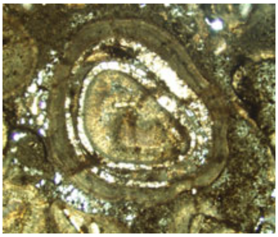

Fig. 6.9 *Qinella* tube–in–tube walls as seen in petrographic thin section. Maximum width of tube 3.8 mm

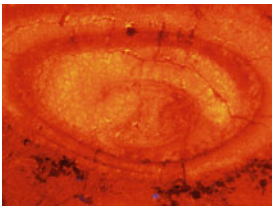

Fig. 6.10 *Qinella* tube–in–tube walls seen in petrographic thin section cathodoluminescence. Maximum width of image 3.7 mm

Sinotubulites are now recognized as distinct taxa (Chen et al. 2007). *Qinella* is a distinct genus as well, and clearly ranges into the Cambrian as shown by the new Death Valley fossils. *Cloudina* also co–occurs with fossils of Cambrian aspect from the Nemakit–Daldyn horizon (Zhuravlev et al. 2012).

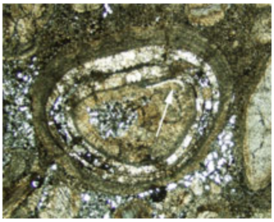

Fig. 6.11 Cross section through a *Qinella* tube, as seen in thin section, with a trilobite "shepherd's crook" (*white arrow*) lodged deeply inside the shell. This trilobite fragment confirms the Early Cambrian age of the *Qinella* fossil. Maximum width of tube 4 mm

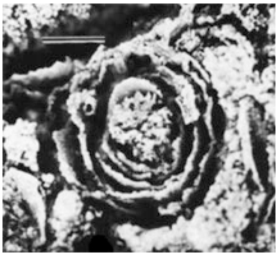

Fig. 6.12 *Qinella* from the Proterozoic La Ciénega Formation of Sonora, México. This was the first published image of *Qinella*, as a "multi–walled, probably tubular fossil from Cerro Rajón" (McMenamin et al. 1983), Sonora, México. Scale bar = 1 mm

Figure 6.11 shows a cross section through a *Qinella* tube, as seen in thin section, with a trilobite "shepherd's crook" (i.e., fragment of trilobite shell from the edge of its carapace) lodged inside the shell (arrow), thus demonstrating its Cambrian age (Cambrian Stage 2/Atdabanian Stage or later). As the fragment is lodged deeply in the interior of the shell, this specimen of *Qinella* cannot represent a reworked or "recycled fossil," that is, a *Qinella* that was eroded out of Precambrian strata and then incorporated into a Cambrian limestone. This is so because the shell interior would have been occluded by Proterozoic sediment before erosion and transport. The abundance of *Qinella* specimens in the Bear Claw Plateau sample argues against this possibility as well. Reworked fossils are rare and often isolated from one another.

The *Qinella* wall structure is manifest as nested, loosely–spaced cylindrical walls of variable thickness. The walls may thin and pinch out against adjacent walls, as seen in both transverse and longitudinal section. This is well displayed by specimens of *Qinella* from the Proterozoic La Ciénega Formation of Sonora, México (Fig. 6.12). *Qinella's* wall structure evidently provided a formidable defense against boring micropredators. The enhanced protection afforded by its multilamellate shell allowed *Qinella* to survive well into the Cambrian.

Evidence for predators drilling into shellfish from the Early Cambrian is well established. Phosphatic tubular shells such as *Hyolithellus* frequently show drill holes from boring predators. Holes are so frequently encountered in *Hyolithellus* that they once constituted part of the description for the genus, the implication being that they were formed as part of the biomineralizing construction of the shell. We now know that they were formed not by the *Hyolithellus* animal, but rather by the predator of the *Hyolithellus* animal (McMenamin 1987).

A mollusk or mollusk–like animal using its miniaturized anterior scleritome, the rasping radula, presumably drilled these holes. The tiny teeth of the radula alone, however, may have difficulty damaging a hard shell, or at the very least drilling through the shell could take a very long time. This suggests that early predators that were able to drill into shells to attack the inhabitants were able to employ both mechanical *and* chemical modes of attack. The mechanical part of the attack would involve a radula that could progressively grind its way through the shell by means of numerous rows of microscopic teeth fashioned from magnetite or other iron–bearing mineral. The chemical part of the attack would involve secretion of acid. If this inference is correct, it represents the first evidence for secretion of acid in the fossil record by an animal. Microbes such as rock–eating bacteria have presumably utilized acid secretion since not long after the first appearance of life on Earth. Secretion of acid by predatory animals would then represent a predator's response to the new animal ability that is most commonly associated with the Cambrian Explosion, namely, biomineralization.

Figure 6.13 shows how this would work. With a cylindrical shell that has wall layers in close proximity, say juxtaposed right against one another, a boring predator will begin its attack on the outer wall. After forming a pit by a combination of mechanical grinding and acid secretion, the pocket formed by the pit becomes a reaction chamber for the acid. With increasing concentrations of acid as secreted by the hungry predator, the bottom of the reaction chamber becomes increasingly effective at weakening and softening the shell. This action continues on into the second wall layer, and then into the third and beyond until the entire shell wall is breached and the prey consumed (Fig. 6.13a).

An attack on the shell wall structure shown in Fig. 6.13b, representing the wall of *Qinella*, proceeds at first in the same way as in the previous diagram, with an important difference. After the first wall is breached, the predator encounters fluid filled space between the outer and the first inner wall. This has two deleterious effects on the attempted murder. First, the radular belt grinder may have difficulty

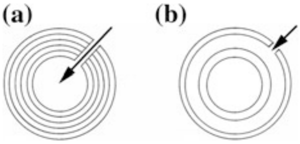

Fig. 6.13 Boring through multilayered cylindrical shells using acid secretions. **a** Walls juxtaposed. Note how a boring organism (*arrow*) is able to penetrate to the shell interior and kill the inhabitant; **b** walls separated by an internal cylindrical space. Note how a boring organism is prevented from boring to the shell interior when it encounters the fluid–filled etch stopgap between shell layers

passing through the hole that was made in the outer wall and gaining purchase on the first inner wall. It might tend to distend though the hole constriction and may not work at all on the far side because it might jam up on the edges of the first hole. It might not reach to the next wall because it is not long enough to span the fluid gap. Second, and perhaps more serious from the point of view of the predator, once the outer wall is breached, the boring acid reaction chamber is destroyed as fluid rushes in and dilutes the acid. The entire defense setup evokes comparisons with clever medieval castle defenses, where there might have been a moat or other unpleasant surprise for the invaders between the inner and outer walls of the castle.

A perhaps better analogy proceeds from the language of nano–fabrication in the semiconductor industry. A layer that prevents further action of an acid is called an etch stop (Oliver 2010). *Qinella* had created the world's first etch stop by neutralizing acid with its inter–layer fluid.

This analysis provides a good explanation for how *Qinella* may have survived the Cambrian Explosion. By means of the relatively simple expedient of increasing the spacing between the cone–in–cone walls of this member of the Cloudinidae (and thus relative to *Cloudina* and *Sinotubulites*), *Qinella* was able to survive the onslaught of dramatically increased predation pressure at the Cambrian boundary. Otherwise successful boring predators simply could not efficiently cut through the *Qinella* tubular shell wall. They spent so much time struggling in frustration during the attempt that they themselves may have been attacked and picked off by other predators.

Three new inferences emerge as a result of this analysis. First, although Cambrian bored shells have been described previously, we may now safely infer that Early Cambrian boring metazoan predators used acid to soften the shells of their victims as they began the attack. Second, *Cloudina*, *Sinotubulites* and all other members of the Cloudinidae except *Qinella* were probably driven to extinction by Cambrian boring predators. Third, *Qinella* itself eventually went extinct, possibly a victim of newly–appearing durophagous predators capable of crushing its thin walls rather than merely perforating its defenses.

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Chapter 7
Sampling Bias

> *Honorable errors do not count as failures in science, but as seeds for progress in the quintessential activity of correction.*
> Stephen Jay Gould (1941–2002)

Abstract How abrupt was the Cambrian Explosion? Analysis of the Lignor-Sipps effect indicates that the burst of new phyla at the Cambrian Explosion was more real than apparent. The reason (or reasons) for this Big Bang of macroevolution remains unexplained.

Particular ancient organisms, such as, for example, *Tyrannosaurs rex*, are more "interesting" to study than others, and hence they have a disproportionate representation in the paleontological literature. Some ancient creatures are more abundant or more widespread than are others, hence they have a better chance of being preserved as fossils. Some organisms are most easily, or perhaps only, preserved at sites of exceptional preservation—the Lagerstätten. These are typically sites of soft-bodied preservation, such as the Burgess Shale and the Chengjiang biota, known for their Cambrian soft-bodied fossils, but other types of exceptional preservation can occur as well, for example in the Permian strata of the Glass Mountains (Sierra del Vidrio), West Texas, USA, where spiny brachiopods (such as *Edriosteges multispinosus*) were replaced by silica. These can be removed intact from the reef limestones, thus providing much more taxonomic information about the brachiopods than would ordinarily be available, as the delicate spines ordinarily break off or are otherwise lost during typical modes of burial and preservation. The specimens recovered in this way are so delicate that they must be transported in a special high-ceiling glass-covered box (Riker mount; Cooper and Grant 1972) to avoid damage.

By means of a phenomenon known as monographic swelling, the published descriptions of the well-preserved Glass Mountain brachiopods led to a bulge in the perceived species diversity of brachiopods during the Permian. In other words, Cooper and Grant (1972) provided an unintentional *false signal for the unwary* of brachiopod species diversity during the Permian, due to preservational bias at the

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Glass Mountain site. Counting of taxa must therefore be undertaken with consummate care (Emig et al. 2015).

This question of taxon counting is closely associated with the paleontological analysis of mass extinction events. In the 1980s, the Earth sciences saw vigorous debate about the mode and tempo of mass extinctions. Were they gradual or abrupt? The end-Cretaceous mass extinction (66 million years ago), famous of course for the demise of non-avian dinosaurs, was a particular focus of abrupt-versus-gradual debate. A literal reading of the fossil record seemed to indicate that certain groups had been in decline or died out before the mass extinction at the end of the Maastrichtian (latest Cretaceous).

This debate was settled by Philip Signor and Jere Lipps in a book chapter that established what is now known as the Signor-Lipps effect (Signor and Lipps 1982). In a nutshell, Signor-Lipps affirms that abrupt mass extinctions will appear to be gradual because of sampling bias. Microfossils such as foraminifera (forams) and pollen can occur as fossils in very large numbers. For example, a cubic centimeter of limestone can contain thousands of forams. By comparison, snail shells will be less common, fish remains even less common, and fossils of large predators such as the Jurassic-Cretaceous marine crocodylomorph *Dakosaurus* or its terrestrial counterpart *Tyrannosaurus* will be rarest of all. In general, the abundance of any fossil type is inversely proportional to its position in the food pyramid, with the keystone predators tending to be the rarest as fossils.

Due to this sampling bias, the fossil record of apex predators is going to be lousy in comparison with that of organisms lower in the trophic pyramid. If a large marine predator and a Cretaceous foram go extinct roughly simultaneously, the last foram fossils will be seen to occur in the last centimeter of Cretaceous marine strata, whereas remains of the last observed large predatory marine reptile might occur meters or tens of meters stratigraphically below the boundary horizon. Thus, because of smearing, the fossil record read literally would misleadingly suggest that the marine reptile had gone extinct considerably before the foram's demise, when in fact the extinctions took place at virtually the same time.

The Signor-Lipps effect has a fascinating and not well-understood historical relationship to analysis of the Cambrian Explosion. It required sleuthing and posing some carefully-worded questions to my colleagues to obtain the full story (McMenamin 2014). The implications of this finding are profound for the paleontological sciences, the Earth sciences, and science in general.

Again, the Signor-Lipps effect explains the tendency of mass extinctions to appear gradual due to differential preservation among organisms of various sizes and abundances. Signor-Lipps can also be applied to estimates of the origination dates of taxa appearing as fossils long after their actual first appearances. Swapping extinction for origination when considering individual lineages, some authors (Buchanan 2002) have facetiously called this second aspect the Lipps-Signor effect. There is also what had been called the Inverse Lipps-Signor effect, where a mass extinction event might seem to be more abrupt that it actually was, based on an abrupt change in preservation potential in, for example, Ordovician graptolites (Belscher et al. 2007; Mitchell et al. 2007).

The Lipps-Signor effect has long been used in attempts to neutralize the threat that an abrupt Cambrian Explosion poses to evolutionary gradualism. Darwin himself argued that a long sequence of Precambrian ancestors to the Cambrian animals might simply be missing from the rock record (this is in a certain sense the ultimate 'missing link' argument). Charles D. Walcott, in an attempt to salvage Darwin's gradualism across the Cambrian boundary, proposed the 'Lipalian Interval.'

This putative major interval in Earth history, which Walcott argued was represented by a gigantic worldwide hiatus or gap (unconformity) in the stratigraphic sequence, supposedly would have contained the animal ancestors had the layers of the Lipalian been preserved. We now know, however, that the Lipalian gap does not exist, because a number of important stratigraphic sequences with fine fossil records are known that are more-or-less continuous across the Proterozoic-Cambrian boundary. The Darwin-Walcott impulse is understandable. The Cambrian Explosion is mysterious, and as Friedrich Nietzsche put it: "to trace something unknown back to something known is alleviating, soothing, gratifying and gives moreover a feeling of power… any explanation is better than none."

Darwin, Walcott and others argued that the incompleteness of the fossil record obscured the assumed long pre-Cambrian histories for animal phyla. In addition to the Signor-Lipps effect and the Lipps-Signor effect, I propose here a new permutation: the Lignor-Sipps effect (Table 7.1).

With the Lignor-Sipps effect, less easily preserved organisms will appear to have originated long after a rapid diversification event because it may take some time for the appropriate depositional environments to arise that can preserve delicate forms representing lineages in the early stages of acquiring hard parts. The temporal smearing of the paleontological record by Lignor-Sipps is a near mirror image of Signor-Lipps, but the smearing pattern may be somewhat different in Lignor-Sipps effect considering delays in the acquisition of skeletons. Lipps-Signor may apply to a few metazoa of the Cambrian Explosion, chitons for example, but the records of many Cambrian higher taxa clearly represent cases of Lignor-Sipps effect. The Cambrian Explosion was therefore *even more abrupt* than suggested by the Burgess Shale and Chengjiang lagerstätten. Estimates of the duration of the Cambrian Explosion must be revised accordingly. We are not dealing with an 80 million year stretch in the Explosion interval as some have argued.

Let's now turn to examination of the historical relationship between the Signor-Lipps effect and the Lignor-Sipps effect. This has potential importance for

Table 7.1 Four paleontological sampling bias effects

Effect	Sampling bias
Signor-Lipps	Abrupt mass extinctions appear gradual
Lipps-Signor	Gradual originations appear abrupt
Inverse Signor-Lipps	Gradual mass extinctions appear abrupt
Lignor-Sipps	Abrupt originations appear gradual

the history of science in the sense of development of an important conceptual framework. The story begins with paleontologist Kraig Derstler.

In 1981 Derstler wrote a chapter for a multi-author volume entitled *Short Papers for the Second International Symposium on the Cambrian System*. Most of the papers in the volume were merely extended abstracts. In September 2014, as I was preparing my talk for the annual Geological Society of America meeting in Vancouver, I wrote to Kraig Derstler asking him some questions about his paper (Derstler 1981). I mentioned that I had a quick question regarding his paper in *Short Papers for the Second International Symposium on the Cambrian System*. On p. 74, regarding his simple diversity experiment, he wrote that the species matrix was randomly sampled (p survival = 0.05). I asked him to clarify: To what did his p survival parameter refer?

Kraig replied that his simulation was done in a short evening and that his memory was clouded with subsequent discussions of the topic with Phil Signor. He said that he thought that it simply meant that each species had a 1 in 20 chance of surviving to a particular time interval. As he only used a few time intervals in the simulation, the probability of survival had to be relatively low.

I replied that that was what I thought he had meant, but that means that after a single interval on average only 1.5 species of the original 30 would be left alive for the second iteration. I asked Kraig if he generated new species to fill the gaps and continue the simulation, or did he mean a different (p = 0.95) probability of survival? I explained that I was preparing to give a talk on paleontological sampling at the Geological Society of America conference, and that I wanted to mention the results that he had obtained in his paper in *Short Papers for the Second International Symposium on the Cambrian System*.

He replied that he had not looked at the paper in several decades, so he went back and "read the darned thing." He wrote that the probability (p) was the probability of collection, and that he should not have called it probability of survival. The "simulation essentially had 30 species that appeared simultaneous at time = 1. All 30 continued through 40 time intervals. That provided 1200 potential 'fossils.'" He then randomly sampled the 30 × 40 array, with each point carrying 1 chance in 20 of being sampled. Before starting the simulation, he assigned randomly each species to one of nine "major groups." He continued by explaining that some of these major groups had a single species, whereas others had up to 7 species. After the sampling, he did not plot species diversity. He wrote that it never occurred to him that anyone would find that interesting, because this, and its mirror image (mass extinction), seemed too obvious.

He continued to say that of "course Phil Signor and Jere Lipps thought otherwise" and a short time later published the mass extinction part of the problem, to Kraig's "great chagrin." Signor had actually read and criticized Kraig's manuscript. Kraig had tabulated the first appearance of each of the major groups, and for the sake of graphical impact, plotted both the first occurrences and a running average to generate the graph in the paper. He ran the simulation a number of times, always with the same result. He elected to publish the simple graph and not to bother about the probability function, because a camera-ready manuscript was due the next day.

Also, he was in a particular hurry because he had a job interview the next day. He concluded by saying that he "was simply demonstrating the possibility that the very sparse fossil record of Cambrian plus Ordovician echinoderms was consistent with all of the major groups evolving simultaneously at the beginning of the Cambrian, yet their first known appearances dragged out over a long interval of time."

I thanked Kraig for his informative answer, and asked one final question. For the 30 × 40 array, how did he arrive at a 1 chance in 20 of being sampled? Shouldn't that be a 1 in 30 chance if the 30 × 40 array is sampled 40 times? I apologized in advance if I was "missing something that should be obvious."

In Kraig's reply he apologized that he has written the reply late at night, and that the odds of sampling were 0.05, or 1 in 20. Therefore, he ended up sampling the array 60 times.

This email exchange was very helpful to me because I was having some trouble following the telegraphic style of Dertler's (1981) paper. The title of his paper was "Morphological Diversity of Early Cambrian Echinoderms." In his simulation, Derstler (1981) utilized thirty "species," all with equal abundance and identical ranges. These were arbitrarily divided into eight 'phyla.' The species counts for each of the 'phyla' were as follows: 9, 1, 2, 5, 4, 2, 3, 4. Derstler (1981) referred to the 'phyla' as eight "unconnected groups." The combination of thirty species with eight phyla created a species matrix. The species matrix was randomly sampled, with the probability of collection for any given species being one in twenty ($p_{\text{collection}} = 0.05$). Derstler (1981) rendered this as $p_{\text{survival}} = 0.05$.

The really striking result from Derstler's (1981) paper was, in his own words, that despite "the simultaneous appearance of thirty species in the unsampled record, the sample shows a gradual rise in apparent diversity… First appearances of the unconnected groups form a single peak on the histogram." The results also showed a gradual rise in apparent species diversity. Derstler used a 12-interval running average for the clade (='phylum') simulation. Figure 7.1 shows Derstler's (1981) original plots of apparent phylum diversity and apparent species diversity.

Derstler's (1981) success with regard to this analysis is surely due in part to the fact that he was a graduate student of David Raup at the University of Rochester (before Raup moved to the University of Chicago). By establishing the Raupian parameters (Raup 1966) Raup had introduced "computers as a key tool for the study of paleontological problems" (Plotnik 2015). This helped to found the "Chicago School" of quantitative paleobiology.

Rumored to have put himself through college playing poker, Derstler recalls that Raup was once asked if he had handled a fossil recently. Raup replied that he kept one in his desk so that he could roll it around once in a while. One day, at the beginning of a talk at Rochester, Raup's advisor at Harvard (Bernie Kummel) handed Raup a fossil and ordered him to have it identified by the end of the lecture. When a Geology Club undergraduate student once invited Raup to participate in a field trip, Raup replied "No, I might get my hands dirty." Clearly, however, Raup's brilliance with quantitative approaches not only helped to found the "Chicago School", but also inspired great work from students such as Derstler (Plotnik 2015).

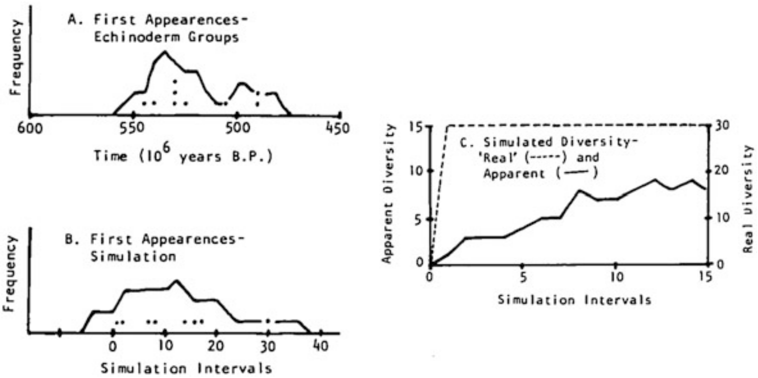


Fig. 7.1 Derstler's (1981) original bivariate plots. His original caption read: "First appearances and diversity patterns of Early Cambrian echinoderms. *A* First appearances of phylogenetically 'unconnected' echinoderm groups. Histogram smoothed with 30-m. y. running average. *B* First appearances of simulated clades. Histogram smoothed with 12-interval running average. *C* Comparison of 'real' (assumed) and apparent (sampled) diversity from simulation"

I replicated Derstler's results using a clade first appearances simulation with a 12-interval running average (Fig. 7.2). Computing power has increased considerably since 1981 so it was fast and easy do this. My curve is very similar to Derstler's (1981) "first clade appearances simulation," and confirms the validity of his results.

Derstler's model is important because it directly addresses a key question: "How abrupt was the Cambrian Explosion?" Derstler concluded (1981), and I agree, that "sampling effects have probably made the Precambrian-Cambrian diversity rise appear much smoother and more gradual than it really was." This conclusion was further underscored and confirmed by the discovery in China of the Chengjiang biota (Xian-guang et al. 2004) in Early Cambrian strata; gorgeously preserved soft-bodied fossils that are every bit as complex (or "advanced") and diverse (in terms of phyla/clades) as the Middle Cambrian Burgess Shale organisms. Thus, the sudden appearance of Cambrian higher taxa (at the beginning of the Cambrian, 542

Fig. 7.2 Replication of Derstler's (1981) results using a clade first appearances simulation with a 12-interval running average. Simulation interval is on the x-axis and clade first appearance frequency is on the y-axis

million years ago) was *an authentic sudden appearance*, a required conclusion after one accounts for sampling bias. This conclusion regarding the evolutionary tempo at the beginning of the Cambrian is startling to say the least from the perspective of a gradualist conventional Darwinian, and Charles Darwin himself would be (in fact he was) the first to admit this.

An additional complication in the Cambrian case is that the animals involved were acquiring skeletons at this time. The Lignor-Sipps effect states that in a sudden origination, sampling effects will make the event appear gradual. This aspect can be seen as the mirror image of the Lipps-Signor Effect (Table 7.1). When an evolving lineage undergoes skeletonization, its preservation potential increases dramatically. If there are delays in the onset of skeletonization, the appearance of particular clades will be delayed, making the event appear even more gradual than was actually the case. This introduces an additional sampling bias not shared in the case of mass extinctions, and thus has no direct counterpart in either the Signor-Lipps Effect or the Inverse Signor-Lipps Effect.

Using a modified Derstler (1981) simulation, we can place quantitative constraints on the speed of the Cambrian Explosion. This revised simulation introduces a time lag (two versions: single big pulse or many small pulses) for phyla/clades that are in the process of developing hard parts and for that reason might show a delayed appearance in the fossils record. Figure 7.3 shows the results of a single large pulse in skeletonization. The modification consists of the following: for the first 30 samplings, odd-numbered clades do not register in the simulation due to delay in the onset of skeletonization in these clades. Figure 7.4 shows the gradual appearance of clades and/or skeletons. Clades appear in order, one at a time after each 8 sampling events. Figure 7.5 summarizes the double bias of the skeleton-origination version of the Lignor-Sipps Effect. The letter "o" denotes the original sampling bias; the asterisk denotes the skeletonization delay sampling bias. The combined effect is to dramatically smear out, or to make to appear gradual, an abrupt origination event. With the skeletonization delay added, Lignor-Sipps effect is inherently a greater magnitude effect than Signor-Lipps, Inverse Signor-Lipps, or Lipps-Signor effect.

We must consider the implications of this for species diversity rise. Three Lignor-Sipps species curves are shown in Fig. 7.6. The first is the original curve

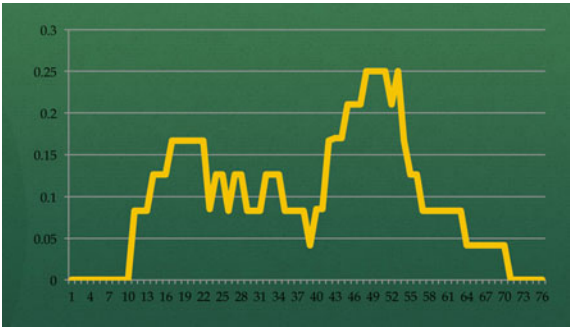


Fig. 7.3 Results of a single large pulse in skeletonization. For the first 30 samplings, odd-numbered clades do not register in this simulation of a delay in the onset of skeletonization. Simulation interval is on the x-axis and clade first appearance frequency is on the y-axis

Fig. 7.4 Gradual appearance of clades and/or skeletons. Clades appear in order, one at a time after each eight sampling events. Simulation interval is on the x-axis and clade first appearance frequency is on the y-axis

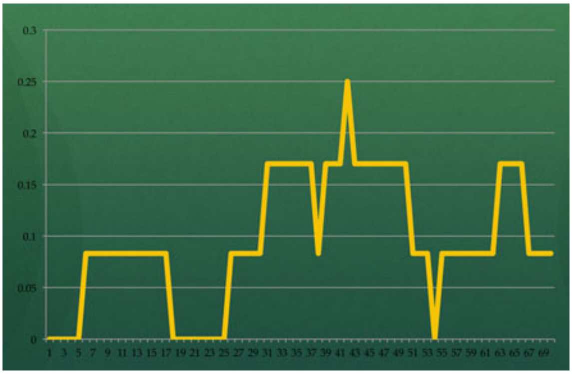


Fig. 7.5 Double bias of the skeleton-origination version of the Lignor-Sipps Effect. The two sampling biases are as follows: *o* original sampling bias; * skeletonization delay sampling bias

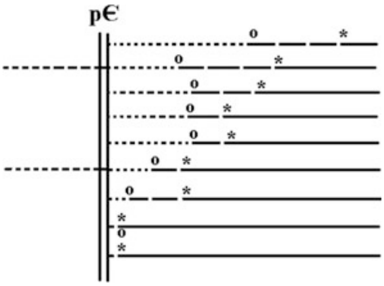
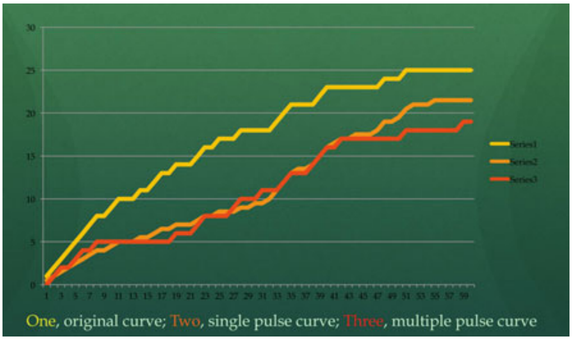


Fig. 7.6 Three Lignor-Sipps species curves. The *upper curve* (Series 1; *yellow*) represents the original curve. Series 2 (*orange*) represents the single pulse curve. Series 3 (*red*) represents the multiple pulse curves. Simulation interval number is on the x-axis and apparent species diversity is on the y-axis



(no skeletonization effect), the second is the single pulse curve, and the third is the multiple pulse curve. The pulse curves are quite similar, and both fall considerably below the original curve. Thus, the species diversity climb is considerably suppressed by delay in skeletonization, and it does not seem to matter if it is a single pulse or multiple pulses.

In the original paper, Derstler (1981) provided for comparison the actual first appearances curve for major echinoderm groups or clades (Fig. 7.1A). He wished to show that this actual data curve was in fact very similar to his first appearances of clades simulated curve (Fig. 7.1B). We may conclude then that the Cambrian event was in fact very sudden due to the match between the actual data Echinoderm Curve, Derstler's (1981) simulated clade curve, and the simulated phylum curve as replicated here. The close match with actual data avoids confirmation bias.

The new simulation presented here is consistent with a sudden Cambrian origination of higher taxa followed by pulses of skeletonization. Delay in the onset of skeletonization (as either single or multiple pulses) makes the apparent 'species' diversity rise appear even more gradual than in the original apparent species diversity curve. The new simulation supports the inference made by Steiner and Maletz (2012) regarding the early record of graptolites and related pterobranchs of Phylum Hemichordata:

> The origin and early evolution of the Pterobranchia as colonial organisms [graptolites], secreting a characteristic housing from organic material, is still unknown. The main reason for the poor record appears to be the difficulty in identifying them unambiguously in many of the famous Cambrian fossil lagerstätten. Pterobranchia likely existed during the Cambrian bioradiation, but a reliable and diverse record is known only from the Paibian of the Furongian Series [Late Cambrian] onwards.

In a similar vein, the contentious Cambrian fossil *Pywackia baileyi* has been identified as the earliest bryozoan (Landing et al. 2010), and this interpretation seems reasonable (Landing et al. 2015) in spite of less convincing arguments that *Pywackia* is in fact an octocoral (Taylor et al. 2013). For both bryozoans and graptolites, then, we see their fossil records extending back into the Cambrian with each new discovery, approaching the Cambrian Explosion at the beginning of the Cambrian, serving as a sort of asymptotic mathematical limit. Interestingly, Steiner and Maletz (2012) see colonial filter feeding in the Cambrian as mainly relying on suspended bacteria and organic matter, as eukaryotic algae such as dinoflagellates were not abundant and were not major primary producers during the Cambrian Explosion.

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Chapter 8
Shell Alignment

> *If we want to attain a living understanding of nature, we must become as flexible and mobile as nature herself.*
>
> Goethe

Abstract What factors influence the postmortem alignment of conical shells? The Hyolith Effect defined here states that if we push any shape parameter subjected to stream flow (actual or metaphorical) beyond a particular threshold, we can expect dramatic system reorientations.

Conical water-dispenser cups have proven very useful for class demonstrations in my geology courses (McMenamin 2001). Rather than providing a model for *Conophyton* stromatolites on the sea floor as you might have guessed, however, we use them to simulate shell orientation in current flows. In the demonstration, twenty-five conical paper cups are attached to strings, and the string is attached to a flat surface such as a cardboard sheet, the floor or a broad table. The cups are scattered about in random orientations at the start of the exercise. Next, we place a powerful fan at the edge of the strewn cup field. I then ask the students to guess whether, once the fan is turned on, the cups will orient with their points upwind or their points downwind. In a middle school presentation, the class will typically be evenly split between upwind and downwind (I have the two groups walk to the walls on opposite side of the classroom, each side representing a particular 'hypothesis team'). My college students are generally better with their initial guesses. Most of these students will end up on the "points upwind" hypothesis team, but even a college class is seldom unanimous at the outset. The students enjoy this exercise, and it is a fantastic vehicle for developing intuition in the physical sciences.

This question of shell orientation (Seilacher 1963) is useful of course for sedimentological studies (e.g., ancient current directions) and taphonomic studies (e.g., what were the conditions of burial?). Although Evans et al. (2015) argue that "nonrandom orientation of any fossil structure in a marine setting is almost exclusively attributed to current activity", other factors such as gravitational settling can also result in shell orientation. With regard to Paleozoic straight nautiloids,

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currents can often be the cause of orientation (Skinner and Johnson 1987), but differential gravitational settling can also also induce a rotational orientation of straight nautiloid shells with the denser siphuncle edge of the shell oriented downward (Reyment 1971). An interesting Ordovician specimen in the Mount Holyoke Paleontology Collection (MHC 3135; orthocone nautiloid internal mold encrusted with the bryozoan *Spatiopora tuberculata*, Ordovician (Richmond-Waynesville Formation), Waynesville, Ohio) consists of a straight nautiloid that sank to the sea floor aperture downward, presumably a gravitational orientation of an empty shell that still had some chamber gas in the tip of the shell, thus causing it to float, and as its chambers slowly filled with sea water, slowly descend to the sea floor in a vertical orientation with the tip pointing up. The chambered shell was buried in this orientation, the chambers were filled with burrow-riddled lime mud that intruded through cracks in the outer shell wall, the vertical shell was partly exhumed on the sea floor by erosion of the surrounding sediment to a level about half way down the shell, and then an encrusting bryozoan colonized the lithified stack of nautiloid chamber internal molds that projected from the sea floor (the outer shell wall was long gone at this point). You can still see a reflection of the curved tracks of the nautiloid septa beneath the encrusting bryozoan colony.

A similar scenario must be invoked, this time with the ‘point’ oriented downward instead of up, to explain the bizarre “nose dive” ichthyosaur remains where the skull and spinal column are preserved vertically in the strata (Wahl 2009). Decomposition gases must have accumulated in the posterior region of the dead ichthyosaur, causing it to orient nose down and descend to the sea floor in that orientation, possibly with sufficient velocity to stab into the sea floor mud, affixing the carcass in a vertical position as it was slowly buried by continued accumulation of sea floor mud.

Analysis of fossil orientation has been applied to Ediacaran fossils. In their article with the evocative title “*Dickinsonia* lift off: evidence for current derived morphologies,” Evans et al. (2015) maintain that *Dickinsonia* specimens with edge pieces missing were partly peeled from their (possibly biofilm-stabilized) substrate. Loose sand slid underneath the uplifted edge of the *Dickinsonia*, causing this portion of the organism to not be preserved, leaving the *Dickinsonia* with an edge clip like a silver coin that has had precious metal removed by unscrupulous shaving of its edge. Evans et al. (2015), after making valid observations about the orientation of the missing *Dickinsonia* edges and their relationship to ambient water currents, incorrectly conclude that this provides evidence for *Dickinsonia* mobility. Rather, this seems to provide evidence for the opposite conclusion, namely, that *Dickinsonia* was stuck to the sea floor rather firmly when it wanted to be, and that swift currents were only able to peel up part of the leading edge of the creature. *Dickinsonia* may well have been a mobile organisms, but the real message of the “lift off” article is that *Dickinsonia* could firmly adhere in place.

Perhaps the best fossil organisms in terms of visually-striking shell orientation are the short-lived tentaculitids, best represented by the genus *Tentaculites*. This is so because currents flowing just above the ancient sea floor easily arranged their long, narrow, annulated conical shells. Structural geologist Michelle Markley calls them "Paleozoic drywall screws." Tentaculitids range in age from Early Ordovician to Late Devonian.

Any relatively major group of marine animals with a first appearance in the Early Ordovician is likely to have a lineage that goes right back to the Cambrian Explosion, as per the sampling bias discussion in the previous chapter. This seems to apply very nicely to tentaculitids; they appear to be descendants of the Early Cambrian small shelly fossil *Olivooides*. Both tentaculitids and *Olivooides* represent problematic groups beset by controversy regarding their biological affinities. Resolving this issue is beyond the scope of this chapter; however, it does appear as if *Tentaculites* represents a member of the *Olivooides* lineage that has undergone neoteny in the sense of developing into an overgrown juvenile. Arguments that *Olivooides* represents a fossil cnidarian comparable to a solitary coral polyp are unconvincing, as *Olivooides* lacks the attachment structure characteristic for polyps of scyphozoans (Dong et al. 2013). It is more likely that both *Olivooides* and tentaculitids represent another type of triploblastic metazoan animal that appeared during the Cambrian Explosion.

Figures 8.1 and 8.2 show bedding plane surfaces covered with fossilized *Tentaculites*. In the Fig. 8.1 sample, the conical fossils are arranged on the sea floor without any obvious orientation. In Fig. 8.2, orientation of the shells is obvious on visual inspection and they seem aligned in an "east-west" direction with regard to the orientation of the photograph. The long axes of most of the shells are aligned, with the apices of some of the shells pointing in one direction, and the apices of the others pointing in the opposite direction, leading to a decidedly bimodal plot of shell orientations.

Measurements of the angular orientation (declination) of the tentaculitid shells are shown on Excel radar plots in Figs. 8.3 (n = 63) and 8.4 (n = 92). Figure 8.4 shows a roughly figure-eight pattern of data, denoting the bimodal separation in the

Fig. 8.1 Bedding plane surfaces covered with fossilized *Tentaculites*. Mount Holyoke College Fossil Collection 4564. Scale bar in cm

Fig. 8.2 Bedding plane surfaces covered with fossilized *Tentaculites*. Mount Holyoke College Fossil Collection 3253. Scale bar in cm

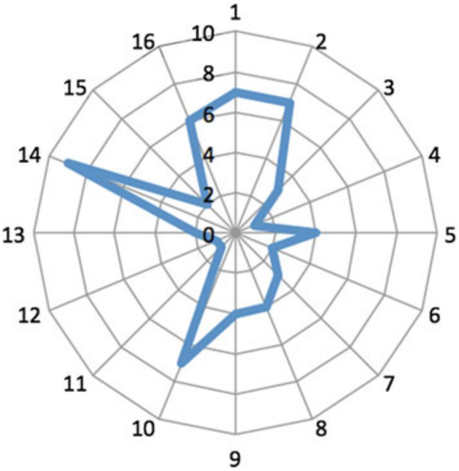

Fig. 8.3 Excel radar plot (n = 63) of tentaculitid specimen 4564. Note cross shape to the radar plot. Hladil et al. (1996, their Fig. 6.20) illustrate a cross-pattern declination plot that strongly resembles the comparable plot shown here

orientation of the conical shells. Curiously, one of the loops is longer (has more data points), possibly suggesting that there was a slight preference in this case for orientation of the cones in one direction rather than with the point in the opposite direction.

Figure 8.3 shows the orientations of the cones in the less obviously oriented sample. Interestingly, the data plot up into a rough cross shape. Hladil et al. (1996) have previously noted such a "cross-pattern" declination in tentaculitids. This type of tetramodal orientation or cross-pattern is commonly encountered in studies of shell orientation. Broad cross-patterns such as the one seen in Fig. 8.3 have been attributed to orientation by currents (Pettijohn 1957; Bouma 1962). Hladil et al. (1996) note that in "patterns reflecting moderate currents, the transverse couple of maxima is represented by rolling elongated shells and the longitudinal ones reflect the tracking positions. With increasing strength of current, the pattern becomes unimodal "comet-shaped" (Nagle 1967), with the maximum in apex orientation upstream." In other words, at moderate current speeds the narrow shells will show a

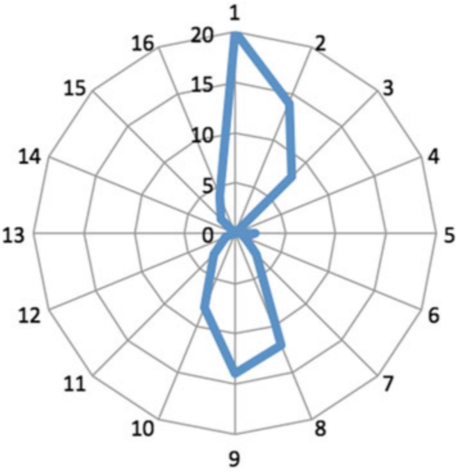

Fig. 8.4 Excel radar plot (n = 92) of tentaculitid specimen 3253. Note the figure eight pattern to the radar plot

bimodal distribution, with some shells rolling (with axis perpendicular to current direction) and others in tracking position with the apex pointing upstream (axis parallel to current direction). At higher current speeds, all the shells shift to tracking position as if to point in the direction from whence the current flows. This generates a comet-shaped unimodal pattern. This is an interesting conclusion that we will explore further in the next example.

Figures 8.5 and 8.6 show a section of Early Cambrian bedding plane surface with oriented hyolith shells. Like *Olivooides*, hyoliths represent another type of enigmatic small shelly fossil well known from Early Cambrian acid residues of limestone dissolution (where their internal molds are common), and also from shales and sandstones. The hyoliths in Fig. 8.5 are preserved in a sandstone collected from the

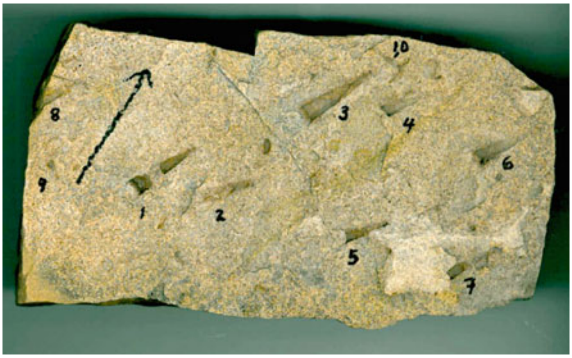

Fig. 8.5 Early Cambrian bedding plane surface with oriented hyolith shells. The arrow on the slab photo is an essentially arbitrary base line from which angular measurements on the shells were made. *Hyolithes* sp. (possibly *H. corrugatus*), Puerto Blanco Formation, Cerro Clemente, Sonora, México, field sample 1 of 5/12/09, greatest dimension of slab 13.3 cm

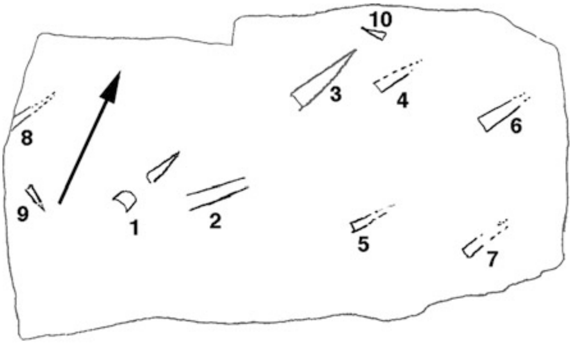

Fig. 8.6 Ten hyoliths as numbered on the slab, photograph and sketch. *Hyolithes* sp., Puerto Blanco Formation, Cerro Clemente, Sonora, México, field sample 1 of 5/12/09, greatest dimension of slab 13.3 cm

Puerto Blanco Formation in Sonora, México. The fossils are preserved on the sole (underside) surface of the sandstone bed.

Hyoliths have a curious conical shell that may be triangular in cross-section but may also be circular in cross-section. In a complete specimen, the opening of the cone is closed by an operculum, and two curved spines called helens (Mus and Bergström 2007) project backwards from the junction between the underside of the cone and the operculum. In addition to possible other functions, helens must have performed a function as hydrodynamic stabilizers, considering as noted above the tendency for narrow conical shells to roll in moderate currents. The triangular and especially the semi-circular cross-sections of some hyolith species may also have, in terms of functional morphology, a hydrodynamic stabilization function as a conical shell with a flat underside is going to be more stable on the sea floor and less likely to roll. Hyoliths evidently did not like to roll when they were alive, but this of course would not stop their shells from doing so after the animal died and its helens fell off. Perhaps a propensity to hydrodynamic stability while living helps to explain the success of hyoliths. Like trilobites, they survived during the entire Paleozoic, only to go extinct in the great End Permian Mass Extinction.

In Fig. 8.6 we see a sketch of the ten hyoliths as numbered on the slab. The arrow on the slab photo is an essentially arbitrary base line from which angular measurements on the shells were made. Eight of the shells show a rather consistent unimodal orientation, whereas two of the shells (numbers 9 and 10) show an orientation very different from the others. All of the shells appear to be conspecific. The shell impressions are not well enough preserved to describe the species; however, there are two other hyoliths on the other side (top bed surface) of the 15–16 mm thick slab. These two hyoliths have the same orientation as most of the hyoliths on the bedding sole surface, and one of the two has six bands (rugae) visible on the shell's external mold, and may belong to the species *Hyolithes corrugatus*. On the sole surface we see impressions of the tops of hyolith shells, on the top bed surface we see the underside impressions of the shells. All specimens again appear to be conspecific. This species of hyolith, then, in addition to having a flat bottom for enhanced stability, also had rugae on the flatter underside, presumably to prevent skidding like the treads on a tire. Sea floor currents, of course, could orient empty shells.

Figure 8.7 shows an Excel radar plot of the sandstone bedding sole hyoliths. It is primarily unimodal, with a tight clustering of most of the data due to the consistent orientation of most of the hyoliths, but there are two small spurs off of the main graph representing the orientations of hyoliths numbers 9 and 10. These are the two smallest hyoliths on the bedding plane surface. The larger hyoliths were oriented with their apices pointing up current, whereas hyoliths numbers 9 and 10 were in orientations roughly perpendicular to the current. This indicates that hyoliths numbers 9 and 10 were rolling rather than assuming the streamlined tracking position with apex pointing upstream. Thus this radar plot assumes the form of the "cross-pattern, or in this case a "three-quarters cross-pattern." The odd shape of the plot is almost certainly due to a limited data set as the sole surface only preserved ten specimens. Had more of the bedding surface been preserved, a full, four-armed cross-pattern would likely have emerged with the accumulation of additional data points.

Recall that hyolith numbers 9 and 10 are the smallest hyoliths on the sole surface. The data set is too limited to make any firm conclusions about a relationship between hyolith size and behavior in currents, however, we may conjecture as a first approximation that the small hyoliths of this species tend to roll, whereas larger hyoliths acquire the tracking position. This conjecture assumes moderate current speed, as faster currents would presumably force all the hyoliths into tracking position. It would imply that, for a given (moderate) current speed, that there is some critical value of hyolith size below which the hyoliths will roll, and above which hyoliths will orient with apex pointing upstream. This concept could lend itself to some very interesting flume tank simulations using model hyoliths of various sizes and shapes.

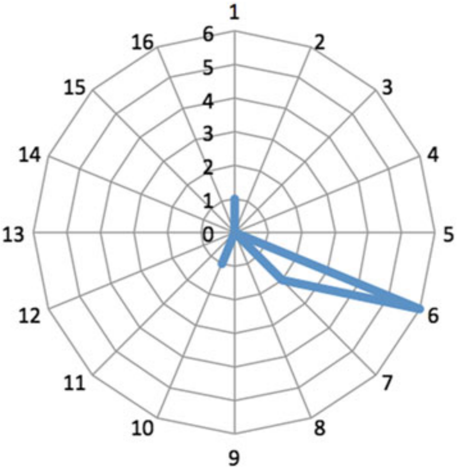

Fig. 8.7 Excel radar plot of the sandstone bedding sole hyoliths

If we assume that size does influence the orienting behavior of hyolith shells, then we could imagine that in a given population of large and small hyoliths, at a given current speed, some will roll and some will track, and the proportion between the two would be a function of current velocity, with all the hyoliths tracking at the highest current speeds. Any such study would assume isometric growth in the hyolith species under consideration. If a hyolith species expressed allometric growth, such as for example the aperture flaring widely in more mature specimens, their hydrodynamics would change accordingly.

Similar considerations apply to variations in hyolith (or other conical shell) shape among different species. Very narrow, tube-shaped cones will be more likely to roll than broader cones where the aperture flares widely. Compare, for example, the narrow *Holmitheca* sp. from Niederfinow, Germany with the broadly flaring *Ceratotheca erratica* from the Kreuzberg section of Berlin (Malinky 2007). Because of their broad flare and obtuse taper, specimens of *Ceratotheca erratica* would tend to first rotate and then assume a stable tracking position as current vectors flow past just like the wind past the nose cone of a rocket. Here we encounter the famous Raupian parameters (Raup 1966).

Raupian parameters are three factors that determine the shape of conical shells. The concept is very useful in invertebrate paleontology (and also in vertebrate paleontology when thinking about the shape of ungulate horns), and can be used to quantify the distinctions between shells of clams, brachiopods, nautiloids, ammonites, and especially snails. The three Raupian parameters are rate of whorl (aperture) expansion, distance from coiling axis, and translation down the coiling axis. All three parameters apply to tentaculitids and hyoliths, however, the curvature or coiling of their shells (if any) tends to be slight (*Ceratotheca erratica* has slight curvature), so for the purposes of this discussion we will ignore the distance and translation coiling parameters and focus on the first parameter, the rate of whorl expansion.

Profound difference in the rate of whorl expansion explains the morphological difference between a clam valve and a snail shell. Aside from this difference, they are otherwise topologically very similar. The offset beak of a clam shows quite a bit of torsion, indicating that like a snail shell the clam shell is in spite of its flat aspect in fact coiling around a coiling axis. The coiling axis is more obvious in snails and it is usually coincident with the spire of the shell. The primary difference between clam and snail in terms of Raupian parameters is that the rate of whorl expansion in snails is low to moderate, whereas the rate of whorl expansion in the clam valve is huge. The aperture outline or generating curve in the clam expands very rapidly, and this is what gives it its flat valve shape.

Typologically speaking, a tentaculitid or a hyolith is very similar to a typical snail shell, as they all have comparable rates of whorl expansion. The primary difference is that the tentaculitid or a hyolith shell does not manifest much coil, or in technical terms its coiling distance value is very high, infinite actually if the shell is in fact a perfectly straight cone.

A narrow straight conical shell (a tentaculitid or hyolith, for example) may have a very low rate of whorl expansion (W), and thus will end up looking like a long tapering hollow pipe. The lower the value of W, the closer the shell approximates a cylinder in form. With somewhat higher W, the straight conical shell will become more triangular (in plan view rather than cross-section this time) due to flaring of the aperture. Shells with low W will clearly tend to roll in a current, and it will require higher current speeds to orient them into tracking position. Shells with high W will be roll-resistant, and will tend to orient to tracking position much more readily than their low W counterparts.

Figure 8.8 shows a plot of this relationship. The x-axis ranges from slow to fast current. The y-axis plots the percentage of shells of a particular size that have attained tracking position with the apex pointing upstream. The upper curve shows that high W shells orient to tracking very quickly and soon plateau at 100 % tracking position. Low W shells will roll until the current speeds become very high, at which point they also will attain tracking position. The shape and inflection of the two curves are theoretical at this point. The next step is to establish the precise track of these curves by means of experimental data. We can say at this point that the hydrodynamic relationships are well understood, and that the experimental curves will have much in common with the theoretical curves as shown in Fig. 8.8.

Although this has not to my knowledge yet been experimentally tested, I predict that the transition from the low W curve to the high W curve will be sudden. There may very likely be some type of threshold effect. In other words, roughly cylindrical shells will remain close to the concave-upward low W line even as W gradually increases. Then, at some critical value of W, the behavior of the shells in a current will suddenly switch over to the convex-upward high W line. There will be very few, perhaps no shell shapes in the central space between the high W line and the low W line. This is analogous with Raupian parameter space, where certain combinations of W, coil distance and coil translation are very rare or simply do not occur in nature.

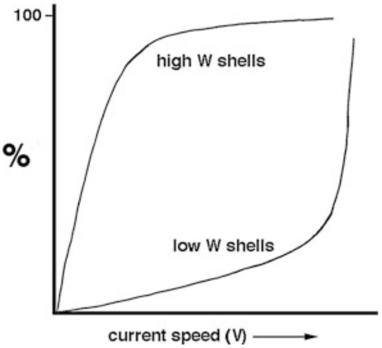

Fig. 8.8 Theoretical plot of current speed versus percentage of conical shells tracking. The x-axis ranges from slow to fast current (*V*). The y-axis plots the percentage of shells of a particular size that have attained tracking position with the apex pointing upstream (%). The *upper curve* shows that high W shells orient to tracking very quickly and soon plateau at 100 % tracking position. Low W shells will also track, but only at higher current speeds (*lower curve*)

An objection could be raised to this set of inferences as follows. Why are cross-pattern rose diagram or radar plots so commonly encountered in shell orientation studies? Would not a cross-pattern plot indicate that shells were falling into the no-man's-land between the high W line and the low W line? To answer these questions, it is enough to realize that natural current flow is pulsational and that current velocities are constantly changing in the majority of situations encountered on the sea floor. The same is true of lake bottoms; sedimentary structures indicative of oscillatory currents (such as symmetrical-crested ripples) are common in lacustrine deposits. Thus, the currents are always shifting from fast to slow in pulses, leaving some of the shells in rolling position and some in tracking position, thus accounting for the frequent occurrence of the cross-pattern plot. It takes a sustained current to orient any particular collection of shells into its equilibrium condition for a given current speed, and such monotonous sustained currents are not the norm in most natural aquatic depositional settings.

I call this the Hyolith Effect, which may be generalized as follows. If we push any shape parameter performing in a stream (actual or metaphorical) beyond a particular threshold, we can expect that dramatic system reorientations will occur. The reorientation of hyoliths due to the Hyolith Effect is in fact 90°, namely, their transition from the low W curve to the high W curve, or alternatively their altered orientation in fast currents versus slow currents. Could the Hyolith Effect be applied to other pressing topics in paleontology? Does the Cambrian Explosion represent a cascade of Hyolith Effects that led to the sudden appearance of new phyla?

If ecosystem engineering (new predators, construction of new niches, etc.) represents the "biotic current," and characteristics inherent to organisms (morphogenetic fields) represent the "shell shape," and both can change independently, then we might expect a complex mosaic of threshold effects of such a nature that they could lead to the appearances of new phyla. Earlier studies suggested that ecosystem engineering alone, namely emergent animals rapidly altering their marine environment and ecology, could explain the Cambrian Explosion (McMenamin and Schulte McMenamin 1990).

In spite of the unprecedented, singular and global changes to marine ecology that occurred during the Cambrian Explosion interval, I no longer believe that ecosystem engineering by itself is a sufficient explanation. The Cambrian animal phyla are too different from one another and appear too quickly. Some other factor must be involved, something that can make profound changes to the otherwise unassailable genomic kernel in very short order. We will return to this conundrum in the final chapter.

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Chapter 9
Deep Bones

> *The weight of the evidence should be proportioned to the strangeness of the facts.*
>
> Pierre-Simon Laplace (1749–1827)

Abstract What killed the giant ichthyosaurs of Berlin-Ichthyosaur State Park in Nevada? The leading hypothesis is that a giant octopus-like cephalopod attacked and killed the *Shonisaurus* ichthyosaurs and dragged their corpses to the Triassic sea floor. The Triassic Kraken hypothesis has survived all tests to date, and currently stands alone as the best explanation for the strange collection of large ichthyosaur bones at Berlin-Ichthyosaur State Park, Nevada.

Monmouth Beach on the south English coast near Lyme Regis is well known for its Jurassic ammonite fossils preserved on single bedding planes. With their coiling axes vertical, most of the shells have roughly the same orientation as exposed on the beach. Branching trace fossils wind their way through the gray matrix between the ammonites. Lower Triassic ammonites of the *Columbites parisianus* zone are known to orient in a similar fashion in the Thaynes Group at Bear Lake Hot Springs, Idaho (Lucas 2010).

Oriented ammonites have also been reported from the Middle Triassic Fossil Hill Member of the Prida Formation (Star Peak Group), of Fossil Hill, Nevada. Unlike the Jurassic ammonites at Monmouth that are laid out flat on a single bedding plane surface, the Star Peak Triassic ammonites are stacked one upon the other in an imbricate fashion (Fig. 9.1; Nichols and Silberling 1977) that indicates the flow direction of an ancient current that was strong enough to orient and stack the fossils. Nautiloid shells (*Nautilus pompilius*) of various sizes require current velocities of 0.25–0.37 m for transport (Wani and Ikeda 2006), and can be reoriented with speeds as low as 0.2 m/s. Current alignment (the stable configuration is with the aperture downstream) happens more easily with large nautiloid shells than with small shells. Sediment erosion around brachiopod shells can cause them to become buried in sediment, and occurs at velocities much less than that required for transport (Messina and LaBarbara 2004).

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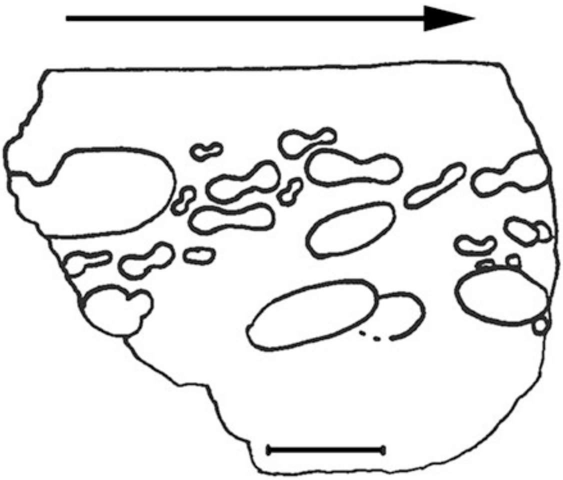

Fig. 9.1 Oriented ammonites seen in section on a polished slab from the Middle Triassic Fossil Hill Member of the Prida Formation (Star Peak Group), of Fossil Hill, Nevada. *Arrow* shows direction of current flow as suggested by the imbricate orientation of the ammonites. Sketch redrawn from Nichols and Silberling (1977). Scale bar = 3 mm

I was first drawn to the Berlin-Ichthyosaur State Park (BISP) to study the sedimentology of the site. My initial concern was to test Jennifer Holger's conclusion that the large ichthyosaur skeletons were deposited in deep water, not shallow water as originally inferred by the distinguished U. C. Berkeley paleontologist Charles Camp, the man who originally excavated the site. After confirming the deep-water nature of the depositional environment, what struck me most about the site was the odd disposition of the ichthyosaur bones. The Berlin-Ichthyosaur State Park Fossil House quarry site shows no evidence for nearshore microbial mat accumulation, and abundant disarticulated crinoid remains as might ordinarily be expected in a Triassic shallow marine limestone deposit are not present as in the Virgin Limestone Member of the Moenkopi Formation, southern Nevada (Schubert et al. 1992).

The *Shonisaurus* skeletons did not show the characteristics I would expect for ordinary decay and disarticulation of skeletons by the action of currents combined with rotting of soft tissue (Foster 2003). There appeared to be a very odd and intentional articulation of the skeletal pieces, and when the implications of this hit home it made what was left of my hair stand on end.

There exists a long tradition in invertebrate paleontology of fascination with gigantism in cephalopods. In a chapter entitled "Class Cephalopoda" in the 1987 compendium *Fossil Invertebrates*, John Pojeta and Mackenzie Gordon devoted a section to the question of cephalopod gigantism and its relationship to Cope's Rule. The concept of an ancient kraken is mainstream invertebrate paleontology, and here is an analysis by the two experts on fossil cephalopods (Boardman et al. 1987):

> Written tales of sea monsters are as old as the ancient Greek epic poems. The source of many of these tales seems to be the larger squids, which are sometimes called kraken, and the larger octopuses, which are sometimes called devilfish… Gigantism in cephalopods has been a recurrent feature…Cope's rule is the name customarily applied to the widespread tendency of animal groups to evolve toward larger physical size… Various lineages have occasionally produced unusually large species that became extinct, but the lineage continued to exist and subsequently produced smaller species.

Our Triassic Kraken hypothesis, presented to the Geological Society of America at its October annual meeting in Minneapolis (McMenamin and Schulte McMenamin 2011), generated an enormous amount of attention on social media immediately after the Geological Society's press release announcing the discovery. As a result, I was invited to speak on the science audio program *Science Friday*. The Triassic Kraken hypothesis triggered a reaction in some people similar to the reaction they might have by reading the following tabloid headline: "Octopus Eats Dinosaur!"—a lurid claim to be sure, but one that is, as we will soon see, literally true.

The Triassic Kraken hypothesis also faced a backlash by a number of skeptical colleagues, and the exchange has developed into what arguably might be called a great geological controversy (Hallam 1989). Whether or not the Triassic Kraken hypothesis is ultimately shown to be correct or false, the hypothesis has unquestionably generated considerable interest. As Quammen (1995) put it, "a good theory, a useful theory, is hard to ignore, because it explains not just facts but a pattern of facts that otherwise seems inexplicable." Our original abstract, entitled "Triassic Kraken: The Berlin-Ichthyosaur death assemblage interpreted as a giant cephalopod midden," read as follows:

> The Luning Formation at Berlin-Ichthyosaur State Park, Nevada, hosts a puzzling assemblage of at least 9 huge (≤14 m) juxtaposed ichthyosaurs (*Shonisaurus popularis*). Shonisaurs were cephalopod-eating predators comparable to sperm whales (*Physeter*). Hypotheses presented to explain the apparent mass mortality at the site have included: tidal flat stranding, sudden burial by slope failure, and phytotoxin poisoning. Citing the wackestone matrix, J. A. Holger [1992] argued convincingly for a deeper water setting, but her phytotoxicity hypothesis cannot explain how so many came to rest at virtually the same spot. Skeletal articulation indicates that animals were deposited on the sea floor shortly after death. Currents or other factors placed them in a north-south orientation. Adjacent skeletons display different taphonomic histories and degrees of disarticulation, ruling out catastrophic mass death, but allowing a scenario in which dead ichthyosaurs were sequentially transported to a sea floor midden. We hypothesize that the shonisaurs were killed and carried to the site by an enormous Triassic cephalopod, a "kraken," with estimated length of approximately 30 m, twice that of the modern Colossal Squid *Mesonychoteuthis*. In this scenario, shonisaurs were ambushed by a Triassic kraken, drowned, and dumped on a midden like that of a modern octopus. Where vertebrae in the assemblage are disarticulated, disks are arranged in curious linear patterns with almost geometric regularity. Close fitting due to spinal ligament contraction is disproved by the juxtaposition of different-sized vertebrae from different parts of the vertebral column. The proposed Triassic kraken, which could have been the most intelligent invertebrate ever, arranged the vertebral discs in biserial patterns, with individual pieces nesting in a fitted fashion as if they were part of a puzzle. The arranged vertebrae resemble the pattern of sucker discs on a cephalopod tentacle, with each amphicoelous vertebra strongly resembling a coleoid sucker. Thus the tessellated vertebral disc pavement may represent the earliest known self-portrait. The submarine contest between cephalopods and seagoing tetrapods has a long history. A Triassic kraken would have posed a deadly risk for shonisaurs as they dove in pursuit of their smaller cephalopod prey.

Ichthyosaur fossils have been known from Nevada since 1868 when miners discovered specimens of what was eventually described as the ichthyosaur *Cymbospondylus* by Philadelphia paleontologist Joseph Leidy. The fossils, primarily vertebral centra, were found by the miners in the New Pass Range, to the north of the present-day Berlin-Ichthyosaur State Park near Gabbs, Nevada. Subsequent discoveries around the turn of the century demonstrated the presence of ichthyosaurs in the West Humbolt Range (Merriam 1902, 1908) near Lovelock, Nevada.

An unusual aspect of Berlin-Ichthyosaur State Park is that it juxtaposes an important fossil site with an historic precious metals mine. The Berlin mine was active from 1897 to 1910 and during that time recovered and processed gold and silver ore. At its peak, the Berlin mining camp employed 300 miners. The stamp mill rock crusher was so loud that it could be heard across the Ione Valley.

It has been widely reported that these miners were the first to report the giant ichthyosaur bones, and this seems reasonable as they would have run across them while prospecting the Union Canyon area for additional occurrences of gold and silver. There is some controversy as to what the miners did with the bones after bringing them back to camp. Some of the vertebral centra may have been used as fireplace hearth decorations, and some were evidently large enough (if rather heavy and thick) to use as dinner plates (Camp 1981), with the amphicoelous (doubly concave) nature of the centra used to keep the food from sliding off the plate.

Stanford University geology professor Siemon W. Muller visited the vertebrate fossil sites in Union Canyon in 1929 and concluded that the remains belonged to large ichthyosaurs. Appropriate scientific attention to the site was delayed, partly on account of its remote location, until the early 1950s. Following in the footsteps of Mary Anning, enthusiastic fossil collector Margaret Wheat of Fallon, Nevada (associate archeologist with the Nevada Museum) convinced a University of California at Berkeley specialist in ancient reptiles, Charles L. Camp (1893–1975), to make the trek to Union Canyon and to see the fossils. Camp was so struck by what he saw that he and fellow Berkeley paleontologist Samuel P. Wells initiated a field research program with a major component of excavation.

The excavations continued intermittently from 1953 to 1965. One of the first published photos of work at the site, by Laura Mills and Margaret Wheat, appeared in the *Fallon Eagle* and was subsequently reprinted in July 1954 in the *Nevada State Journal* (Fig. 9.2). The photo shows seven or eight large vertebral centra

Fig. 9.2 Early excavations at the future site of Berlin-Ichthyosaur State Park. Shown in the image are S.P. Welles (*right*) and C.L. Camp (*left*). The vertebral centra shown here are reported to have belonged to a 11 m long ichthyosaur. Photograph by Laura Mills and Margaret Wheat

projecting from the rock as the researchers excavate the matrix surrounding them. Camp's excavation uncovered the remains of more than 40 ichthyosaurs. This led eventually to the establishment of Berlin-Ichthyosaur State Park and the designation of *Shonisaurus popularis* as Nevada's state fossil. The establishment of BISP was undertaken with significant public support. Miller (1963) wrote that: "Today there is urgent need for some important scientific work to be completed at [Berlin-] Ichthyosaur, a final description of the bones and an assessment of their place both in the paleosystematics of evolution and in paleoclimates." At one point a state bureaucrat accused Camp of misusing a state park commission vehicle and gasoline for "pleasure trips to Lake Tahoe and Virginia City," but Camp was later cleared of these baseless charges (Hulse 1957). A bronze plaque honoring Camp was installed at the Fossil House in 1966.

An impressive A-frame Fossil House shed built by Nevada to protect the Fossil House Quarry was joined by the nearby installation in 1957 of a life-sized reconstruction—as a concrete bas-relief—of a swimming ichthyosaur. The famous paleoartist and sculptor William Gordon Huff designed the swimming shonisaur bas-relief. The 17 m length of the bas-relief, currently a favorite photo-op at BISP, is now considered to be somewhat too large to depict the ichthyosaurs at the site. The actual ichthyosaurs in the Fossil House only reached approximately 14 m.

Camp originally described three species of *Shonisaurus* from the site, *S. silberlingi*, *S. mulleri* and *S. popularis*. There seems to be a good deal of intraspecific variability in the morphology of individual bones in these ichthyosaurs, however, so the current consensus is that they all belong to a single species. *S. mulleri* and *S. popularis* have thus been synonymized into the single species *Shonisaurus popularis*. This leads to the key observation that all of the ichthyosaurs preserved in Union Canyon belong to a single species. Not a single additional type of marine reptilian remain has been described from the site. This suggests that the BISP ichthyosaurs lived in a particular environment, such as open oceanic deep water, that excluded other types of Late Triassic marine reptiles. These latter are not even seen as rare occurrences at BISP.

One puzzling aspect of the research at BISP is that the bulk of Camp's research on the ichthyosaurs was published posthumously. Camp was an active and accomplished vertebrate paleontologist and ancient reptile specialist, and even after accounting for chronic illness later in life it seems strange that he published so little on an excavation and research program that occupied several decades, particularly considering its importance for our understanding of ichthyosaur paleobiology. Perhaps Charles Camp was taken aback by the exceedingly odd characteristics of the site ("peculiar" in his phrase). It seems reasonable to conjecture that he was never able to resolve a series of important questions about the site to his own satisfaction before he died. In any case, we are greatly in his debt for bringing these exceptional fossils (Bottjer 2002) to view and helping to preserve the site in perpetuity.

Perhaps the greatest conundrum regarding the site is the depositional environment of the strata that entomb the *Shonisaurus* ichthyosaurs. Curiously, the first published suggestion that the Luning Formation at this site represents a deep water deposit appeared in a newspaper article (Anonymous 1954) in the *Nevada State Journal* on Sunday, 4 July, 1954. Regarding the ichthyosaurs, the paper reported (p. 8) that: “The giant reptiles were rulers of the ancient seas, and, for reasons not determined by the present expedition, congregated in the region being explored. When they died in the deep waters of the area, their bodies decomposed, settled to the ocean floor and were slowly covered by silt. The deposits gradually hardened into siltstone or limestone and the bones became petrified.” Luning Formation strata deposited in shallow water do occur, but far to the south of the Berlin-Ichthyosaur site (Sandy and Stanley 1993).

At least nine gigantic ichthyosaurs are preserved at BISP in a rock layer belonging to the Shaly Limestone Member of the Luning Formation. The animals reached approximately 14 m in length. They are available for public viewing at the Fossil House Quarry at BISP. Analysis of the fossil site has shown it to be a deep-water deposit (Holger 1992), thus invalidating Camp’s (1980) original hypothesis that the fossil bed represented an ichthyosaur mass-stranding event. Holger’s (1992) study left unexplained, however, exactly how it came to be that nine or more giant *Shonisaurus* ichthyosaurs sequentially accumulated at virtually the same spot on the Triassic sea floor.

A number of factors have complicated the interpretation of the site. First, the permineralized bones are very similar in color to the surrounding matrix, so although the outlines of individual bones are clear enough, they are somewhat difficult to photograph because there is not much contrast with the background. Second, after being excavated, the bones were sandblasted to clean them off and this in some cases removed their outermost surface. It is still possible to determine which bones are more weathered and which bones are less weathered, but the sand blasting has complicated the effort to do so.

The paleontological conundrum was crying out for an unconventional new approach, in other words, a new attempt to solve the problem. Immediately after my first visit to the site, and on reviewing my digital photographs back in our hotel in Reno, I was struck that the bones at the Fossil House Quarry appeared to have an odd arrangement that was not the result of mere passive disarticulation, nor different degrees of passive disarticulation of the skeletons, nor displacement of the bones by currents. There appeared to be both linear and clustered geometric arrangements of the vertebral centra that required some agency for moving and placing the bones, an agency that was something other than gravity or current flow. There is a common assumption in the science of taphonomy: “The nonrandom orientation of any fossil structure in a marine setting is almost exclusively attributed to current activity” (Evans et al. 2015). How many fossil shell concentrations (Kidwell et al. 1986), commonly seen in marine strata, have a component of cephalopod construction, as in, represent piles of shells that are the remains of octopuses’ meals? It may be possible to address this question by examining the species composition of these shell beds; shell accumulations predominated by favored molluscan prey of octopus may in fact represent ancient shell middens, and it may very well be possible to make reasonable inferences in this regard from evidence preserved in the shell bed fossil record.

Fig. 9.3 The Specimen U array at Berlin-Ichthyosaur State Park, Nevada. The largest vertebral central approximately 20 cm in diameter

The water flow/current assumption is not warranted at the Fossil House site. I was especially struck by the Specimen U array of bones at the site. Something was wrong here; the pattern was not hydrodynamically stable and it looked like the suckers on a cephalopod tentacle. Is the resemblance is more than mere coincidence?

McMenamin and Schulte McMenamin (2011) hypothesized that the nine gigantic ichthyosaur fossils were captured and transported by a gigantic cephalopod (a "Triassic Kraken"), that killed the marine reptiles and then dragged their carcasses back to its lair. The giant cephalopod then proceeded to arrange the bones of its victims into almost geometric patterns, some of which resemble the sucker arrays on cephalopod tentacles (Fig. 9.3). It turned out to be fitting to choose the year 2011 to announce our idea, as it was the 200th anniversary of Mary Anning's discovery of the first marine reptile skeleton known to science (Torrens 1995; Kear and Budd 2014), the giant Jurassic ichthyosaur *Temnodontosaurus platydon*.

A YouTube video from the Seattle Aquarium, showing a Giant Pacific Octopus (*Enteroctopus dofleini*) attacking and killing a shark, lent widespread credence to the hypothesis. Even skeptics were willing to admit the general plausibility of the idea. As Hill (2011) pointed out:

Table 9.1 Geoglyph and related terms

Term	Definition
Mechanoglyph	A sedimentary structure on a bedding plane surface formed by non-living processes such as wind or water currents
Bioglyph	A sedimentary structure formed on a bedding plane surface by living processes such as the locomotion or burrowing activities of animals
Positive geoglyph	A motif or design formed by intelligent life by alignment of materials on a bedding plane surface or ground surface
Negative geoglyph	A motif or design formed by intelligent life in a desert land region by moving patinated rocks and exposing ground surfaces lacking desert varnish to form the pattern

> [S]tranger things have been known, and if nothing else the claim carries something to fuel the imagination, and test out the veracity of the scientific method in clearing this debate up. In the meantime, what we can safely say is that octopus dragging down large, ocean-going predators is nothing new or novel, although it was unexpected for many years until one public aquarium decided to film what was happening to their sharks in a large aquarium.

To date, over 300 news and analysis articles on the subject have appeared on line and in print sources. Many of these are rehashes of the GSA press release, and as of this writing (December 2015) they continue to appear.

The most controversial part of our hypothesis was the idea that the pattern created by the hypothesized giant cephalopod was not merely a geometrical pattern made by the cephalopod (geoglyph), but also a possible example of self-portraiture that intentionally represents the suckers on the cephalopod's tentacles. Table 9.1 shows the distinction between a mechanoglyph, a bioglyph (Mikulás 1998), a positive geoglyph and a negative geoglyph.

The Triassic Kraken debate is thus twofold. The first part considers whether the death of the *Shonisaurus* ichthyosaurs may be attributed to repeated attacks by a giant Triassic cephalopod. The second part considers whether the several "Specimen U"-type bone patterns that have been discovered to date (as described below) should be considered as positive geoglyphs or as merely collapse- or current-induced mechanoglyphs.

The Triassic Kraken hypothesis is in fact an extension of the great Seilacherian research program (named for the distinguished German paleontologist Adolf "Dolf" Seilacher) that sees ichnofossils as fossilized behavior. A geoglyph is a type of trace fossil. Once alerted to the new hypothesis, Seilacher seemed intrigued by the Triassic kraken and noted that the bone arrangement has indeed "never been observed at other localities." In one of his last communications to me, Seilacher wrote (email from geodolf@gmx.de on October 29, 2011):

> Through Dave Raup we learned that you are giving several lectures at the GSA… [your ideas about the ichthyosaurs] will hopefully spark new research. It could extend to the possibly analogous case of Jurassic ichthyosaur skeletons in Germany. They are restricted to better known Lagerstätten in stagnant, non-benthic basins that received most sediment through muddy turbidity currents. Therefore fossils, including ammonites, tend to be

> current-aligned in an otherwise quiet body of toxic water. The following questions should be kept in mind: (1) Is autochthonous benthos associated with the Nevada skeletons, maybe only in the form of trace fossils? (2) Even a completely soft-bodied octopus needs hard jaws. They should be found if horny material was not destroyed by bacteria. (3) Why did the bones around the biserial vertebrae remain undisturbed? Could this arrangement also result from compaction? It has never been observed at other localities and could be experimentally tested.

In this one of his last scientific communications, Seilacher once again demonstrates his clarity of thought and penchant for careful investigation wedded to a creative approach that was uniquely characteristic of his work. Seilacher notes that Jurassic ichthyosaur skeletons in Germany, which may provide analogous examples, occur in stagnant basin strata devoid of sea floor animals. Such sites received most of their sediment via muddy turbidity currents. Ammonite fossils at these sites are, on occasion, current-aligned in an otherwise quiet water setting in a body of stagnant water.

Seilacher wonders, first, are there fossils of seafloor animals associated with the Nevadan ichthyosaur bones? Second, even an entirely soft-bodied cephalopod would still need a horny jaw, and assuming that it was not destroyed by bacteria, might it still be possible to find a fossil of its beak? Third, why did the bones near the critical Specimen U biserial vertebral array remain undisturbed, and could the arrangement possibly be due to compaction?

The strata of the *Shonisaurus*-bearing Shaly Limestone Member of the Luning Formation in Nevada might very well be compared to the famous Jurassic fossil beds near Holzmaden, Germany (Gall 1983), but they might also be compared to the muddy strata appearing as parallel-bedded lime mudstones of Lefkara, southern Cyprus. Stow (2006) interprets the Cypriot strata as alternating between distal turbidites and open-water sedimentation (pelagites) in a deep-water slope to basinal setting.

Referring to the Cypriot strata, Stow (2006) notes that “the distinction between turbidite and pelagite is often very difficult to make… as is the case here.” Similar considerations would apply to the Shaly Limestone Member of the Luning Formation. In any case, the sedimentology of the Shaly Limestone Member is rightly interpreted as representing a deeper-water setting. Essentially the same depositional setting in inferred for *Shonisaurus* specimens of Hound Island, southeastern Alaska (Adams 2009, his “deep-water Facies 2”). Sediment analysis at the Nevada park indicates that the site was deep (probably 200 m or more), and that local marine depth had been increasing right up to the time that the bones were buried (Silberling 1959).

It now appears that we can confidently rule out a shallow water environment for the BISP fossil site. Turbidite flows can undoubtedly align ammonite remains, as seen in Britain, Germany, Nevada and elsewhere, but whether or not such deep water flows could arrange large, dense ichthyosaur bones into biserial accumulations seems highly unlikely. First, Martill (1993) calculates that very slow currents (0.2–0.4 m/s) over unconsolidated substrates would be sufficient to displace ichthyosaur paddle bones and ribs, but such slow currents would probably not be able

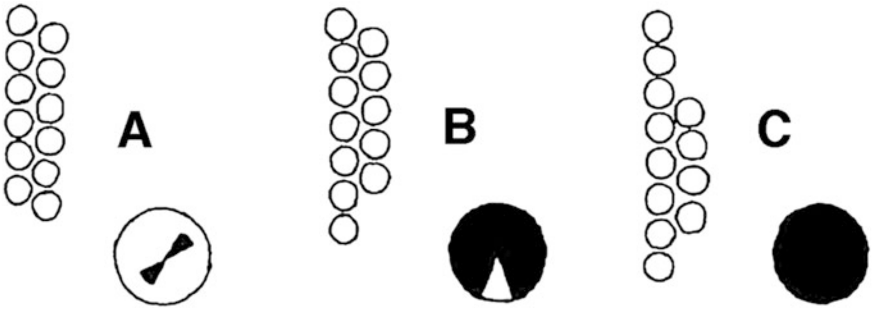

Fig. 9.4 Hydrodynamic instability considerations of the biserial array. The *three rose* diagrams show, in each of the three vertebral centra configurations, the possibility of current displacement of the array by currents strong enough to displace a single centra. Cases *A* and *B* are hypothetical, and case *C* is what actually occurs in the Specimen U array. The more the rose diagram is filled in (*black color*), the more easily disturbed by current is the array. Thus, case *C* (the Specimen U array) is the most easily disturbed by currents

to displace large vertebral centra. Furthermore, the biserial vertebral array in Specimen-U is in a hydrodynamically unstable arrangement, regardless of inferred current direction.

A geometrical demonstration can show the hydrodynamic instability of the biserial array at Berlin-Ichthyosaur State Park with regard to currents fast enough to displace ichthyosaur vertebrae. As seen in Fig. 9.4, Case A is the most hydrodynamically stable. For the sake of discussion, we will consider north to be at the top of the diagram. Only currents from the northeast and the southwest, of sufficient force to displace ichthyosaur vertebral centra (a relatively dense bone type, shaped like a hockey puck), have much chance of displacing the bones, and initially only the ones on the ends of the array are in danger of thus being displaced. Incidentally, these types of vertebrae, with inwardly dished surfaces on opposite sides, are called amphicoelous vertebrae. They are characteristic for blue water, open ocean swimming marine tetrapods (Motani 2000), again in accord with the deep-water interpretation.

The rose diagrams in Fig. 9.4 plot the orientations of competent currents, with the center of the diagram representing the strongest currents and the perimeter of the diagram representing the weakest currents that could move a vertebral centra.

Case B has a dangling vertebral centra on its bottom end, hence it is safe from displacement only from a relatively narrow wedge of current directions that come from north of the array and would flow around the array like currents moving along the streamlined body of a fish. In this case the dangling vertebra is roughly streamlined like the tail of a fish.

Case C is the array actually seen at Berlin-Ichthyosaur as Specimen U. With dangling vertebrae at both ends, any competent current (be it from turbidity current influx, shelf-edge contour currents, etc.), from any direction, is going to displace one or more of the bones; hence the entire rose diagram is filled in.

It is virtually impossible that currents arranged the biserial array seen in Specimen U. This demonstration considers currents that are linear in terms of their trajectory. Non-linear currents, such as swirling currents or gyres, would be even less likely to form the biserial array seen in Case C (Specimen U; Fig. 9.3).

This demonstration can also be given in terms of probabilities. The probability of displacement (PD), or tendency to displacement, by currents in a random set of directions, in Case A, is approximately

$$\mathrm{PD} = 60/360 = 1/6 = 17\,\% \tag{9.1}$$

The probability of displacement in Case B is

$$\mathrm{PD} = 320/360 = 8/9 = 0.889 = 89\,\% \tag{9.2}$$

The probability in Case C, the actual case is

$$\mathrm{PD} = 1.0 = 100\,\% \tag{9.3}$$

Once again, the probability that currents assembled the Nevada array is virtually zero. Even in the unlikely event of two spiral current bores, of the type known to be responsible for forming the elongate grooves called flute casts on the sea floor, that happened to converge along a center line to push material to the boundary between the spiraling currents (analogous to converging circulation cells in the Sargasso Sea), Case C would still be impossible because we would expect the dangling vertebrae on both ends of the pattern to align along a boundary line (or line of symmetry along the long axis). What we see instead is that they are oddly displaced to the left side.

Thus, there is virtually no possibility that currents formed Case C. The triangular neck vertebra on one end of the Specimen U array is in a particularly precarious position, with only one point of contact with an adjacent centra and two corners of the triangle exposed to torque by current flow. The likelihood of the neck vertebra being displaced by current is particularly high, especially considering its position on one end of the Specimen U array.

We can take this analysis one step further by applying the results of studies on the interaction of flowing water and sessile organisms (Koehl 1982). Adult *Shonisaurus* vertebral centra are large enough to experience *form drag* in fast flow, in addition to surface or skin friction that would also be experienced by smaller objects. As Koehl put it (1982), "The magnitude of form drag is proportional to the area of the body and the square of the velocity, and so a fairly small increase in length or velocity can lead to a comparatively large increase in drag form." The amphicoelous shape of the vertebral centra adds additional surface area in comparison to a flat-ended cylindrical object, and form drag on the centra is higher as a result. Form drag increases markedly with increase in water velocity. Koehl notes that the lift force "is not always upward; it can be at any right angle to the flow." Thus there is a fan-shaped array of right angle displacement vectors attending the upper surface of a prostrate vertebral centra in fast flow, and this infinity of vectors will have a strong tendency to displace various centra into a disorganized variety of different orientations. The likelihood of such drag force vectors orienting a collection of centra into a geometric pattern is virtually nil, and the same is true of lower current speeds as demonstrated in Fig. 9.4.

Each individual disc in the array is embedded into the matrix, and there are no associated external casts of nearby discs, therefore no discs were removed from the array subsequent to fossilization. Passive disarticulation of the skeleton after decay of soft tissues would lead to a much less ordered arrangement (as is seen in other places in the Fossil House display at BISP), for in nature systems go from more ordered to less ordered states, not the other way around (Pappas 2013). Organization of the bones by seismic disturbance is implausible because seismic shaking would be far more likely to disrupt rather than to construct any geometric pattern unless the bones were in, say, a dish- or trough-shaped depression on the sea floor. Kelley et al. (2015) have attempted to argue that what is seen at the Fossil House quarry is merely different stages in passive skeletal disarticulation as the skeletons fell apart and collapsed. The Pyenson lab explanation (Kelley et al. 2015) is too facile, and is a mismatch to the evident imparted order of disarticulated skeletal fragments; indeed, *the initial observation of imparted order was what necessitated the Triassic Kraken hypothesis in the first place*. Kelley et al.'s (2015) argument also provides no explanation for the broken ribs of the shonisaurs as described below.

I suspect that Camp (1980, 1981) was perplexed by the patterns of apparent imparted order among the disarticulated bones, and this may explain why his major article on the site was not published during his lifetime. In his posthumous paper, note Camp's (1980) usage of the word 'peculiar': "their peculiar manner of death and burial are questions demanding attention… accumulations and 'concentrations' of material, are evident… [this] must indicate a peculiar selective agency operating continuously." I agree with Camp's (1980) inference of a *peculiar* selective agency that operated continuously; if true, the concept rules out discrete-event mass mortality involving blooms of toxic algae.

The toxic algae hypothesis is mentioned by both Camp (1980) and Holger (1992), but without much conviction. Balini et al. (2014) also mentioned this hypothesis, but without providing supporting evidence:

> The abundance of articulated, closely spaced *Shonisaurus* specimens… may have been induced by algal blooming. Although we do not have supporting evidence, this hypothesis should at least be considered. Harmful algal blooming (HAB) is regarded as one of the most common natural causes of mortality events of marine vertebrates… Further investigation is necessary at BISP in order to test this hypothesis, whose weak point may be the relatively deep water deposition of ichthyosaurs in contrast with the supratidal stranding reported for cetaceans and fishes, and the monospecific composition of the BISP vertebrate fauna.

It is curious that Balini et al. (2014) favor the algal bloom hypothesis without supporting evidence while discussing the evidence that actually favors the Triassic Kraken hypothesis (i.e., deep water deposition, one marine reptile species recorded). Indeed, the deep-water origin of the site precludes a toxic algae explanation, as harmful algal blooming is a phenomenon of relatively shallow marine waters.

Phytotoxin-killed whales tend to disperse widely (Geraci et al. 1989). Also, the monospecific composition of the marine tetrapod fauna works against the HAB hypothesis, as algal toxicity is capable of killing any number of marine reptile species, and yet only *Shonisaurus popularis* is seen at Berlin-Ichthyosaur.

An ichthyosaur site to the south of Nevada sheds light on this last point. The ichthyosaurs *Shastasaurus altispinus* and *Toretocnemus californicus* both occur in the Antimonio Formation (late Carnian, Dilleri Zone) in the northern part of the Sierra del Alamo, northwestern Sonora, México. Although close in age to the Luning Formation in Nevada, the Antimonio Formation is a shallower water site as indicated by the presence of hummocky sandstone horizons (Lucas and González-León 1995). One of the high energy, hummocky horizons itself has yielded ichthyosaur remains. Although the ichthyosaur remains are comparatively fragmentary, multiple genera and species of ichthyosaur have already been recognized in the Antimonio Formation, in contrast to the Luning Formation with many ichthyosaur fossils but only a single species. The deep-water habitat of the Luning Formation may have acted as a filter that excluded other types of marine reptiles, hosting only a single species (*Shonisaurus popularis*) that could survive in a blue water open ocean environment.

One might argue that some sort of preservational bias is at work, eliminating the once-present remains of other marine reptile species. Indeed, other types of marine reptiles should be more abundant than even just one or two specimens, but puzzlingly none have yet been reported. Even when Mesozoic marine reptiles are dominated by particular genera, there remains a significant fraction (42.3–21.8 %) of other taxa (Kiernan 2002). This strongly suggests that the shonisaurs were hunting in an aquatic environment that precluded all or most other marine reptiles of the Late Triassic. If they were deep-water divers, as the sedimentological evidence would seem to suggest, then this is exactly what would have brought them into the territory of, and into contact with, large, deep-water cephalopods.

A further piece of evidence favoring an open marine deep-water habitat for the Nevada *Shonisaurus* involves the structure of the shonisaur eye. Our knowledge of the *Shonisaurus* eye comes from a single sclerotic plate discovered by Camp (1980). The piece of bone was found lying loose in matrix near the skull of the Specimen A ichthyosaur in Camp's Quarry 5 at BISP. The sclerotic plate was found near the orbit or eyehole of the Specimen A skull. Camp (1980) reports:

> [The] single complete sclerotic plate… is thin and flattened distally and much thickened at its pupillary border. Its outer curvature and length would indicate an eyeball with a diameter of from 18 to 22 cm, probably the largest eye on record. Yet this eye would not have filled the orbit which had a diameter of 35 cm or more, and was comparatively small in respect to the size of the skull.

Camp (1980) calculated from the size of this single plate that there "would have been approximately 12–14 scleral plates" in the sclerotic ring that would have formed part of each eye, and that each eye would have been approximately 20 cm in diameter. In a rare mention of a possible deep-water habitat for *Shonisaurus*, Camp (1980) continues: "The large eye may have been useful in pursuing food in deep and dark (or murky) waters." We can further infer that shonisaurs relied on sharp vision to locate their prey, and this would have been the primary method for them to locate food in the absence of any evidence in shonisaurs for cetacean-style echolocation ability.

It is important to note that the cephalopod eye is vastly superior to the tetrapod eye, especially in deep water. This is so because the vertebrate eye has blood vessels in front of the retina, whereas the octopus eye has the blood vessels behind the retina, a more advantageous configuration especially in lower light conditions. The eyes of deep-water cephalopods are specifically suited for such conditions. The eye of the Colossal Squid *Mesonychoteuthis hamiltoni* is the largest eye ever recorded in the animal kingdom, measuring 28 cm across.

Some post-Triassic deep diving ichthyosaurs, such as the Jurassic paripelvian (reduced pelvis; Motani 2009) ichthyosaur *Opthalmosaurus* ("eye lizard") also developed large eyes, up to 23 cm in diameter. Motani et al. (1999) note that there "is a poorly known paripelvian ichthyosaur more than 15 m long, so the largest ichthyosaurian eye was probably more than 30 cm in diameter." These more advanced (paripelvian) ichthyosaurs presumably had better sensory equipment for deep dives than did the shonisaurs, who represented a clade that was still relatively new to the deep diving strategy. Clearly, however, creatures such as *Opthalmosaurus* were relying on vision rather than other sensory modalities to capture prey.

Shonisaurs, and the later paripelvian ichthyosaurs for that matter, had no cetacean-grade spermaceti echolocation/sonor, and would thus have been at a decided sensory disadvantage in a deep-water battle with a giant color- and shape-shifting cephalopod. A prominent discontinuity occurs in ichthyosaur evolution across the Triassic-Jurassic boundary, with the more "primitive" (and hence more easily killed by large cephalopods) ichthyosaurs occurring before the boundary, and the faster paripelvian (with a reduced pelvis to improve speed and to help them chase their faster cephalopod [belemnite] prey; Klug et al. 2016) and presumably more capable ichthyosaurs occurring in the Jurassic and Cretaceous; Thorne et al. 2011). Cephalopods such as octopus and squid are able to modulate their surface coloration by means of chromatophores that render them virtually invisible at depth.

The shonisaur feeding dive may have been slow, and the ascent "leisurely" (Rothschild et al. 2012) meaning that they had to hold their breath longer than later ichthyosaurs. Evidence for vascular necrosis associated with caisson disease (bends) has not been observed in Triassic ichthyosaur remains. A slow ascent would also place them at greater risk for ambush by a deep marine predator. A specimen from of the paripelvian ichthyosaur *Ichthyosaurus* cf. *I. breviceps* the Holzmaden in Germany has had its neck broken and its head twisted around 180° from its natural position (Fig. 9.5). Perhaps this animal ran afoul of the powerful arms of a Mesozoic octopus-like cephalopod.

The question of in situ benthic animal fossils in association with the Nevadan bones is an important one. Benthic animal fossils are rare at the site, although some brachiopods and flat clams (halobiids such as the genus *Halobia*; McRoberts 2000) have been reported from this horizon in the Luning Formation. No trace fossil burrows are known from the Fossil House Quarry, but in the absence of sandy

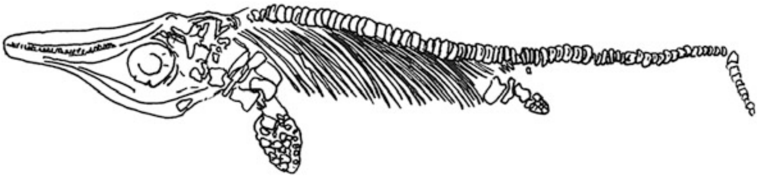

Fig. 9.5 *Ichthyosaurus* cf. *I. breviceps* Owen, 1881. Holzmaden strata (Schomberg Quarry); sketch from specimen in private collection of P. Reiter. Length of skeleton 1 m

turbidite layers to cast the underlying traces, these would not ordinarily be expected to fossilize. Bone borings possibly attributable to the marine boneworm *Osedax* do occur on one of the skeletons outside of the fossil house. Modern *Osedax* has a bathymetric range down to 3,000 m (Vrijhenhoek et al. 2009).

The depositional setting may have been one that experienced reduced oxygen levels, as some organic matter is visible in the rock thin sections. The environment, however, was evidently not greatly anoxic, because the mudstones and micrites are light in color. Modern vampire squids (*Vampyroteuthis*) are able to thrive at dissolved oxygen levels as low as 3 %.

Giant Cretaceous squids (such as *Tusoteuthis*), reaching lengths of up to 11 m, are assigned to the vampire squids because of similarities in the shape of their squid pen (gladius) to that of *Vampyroteuthis*. Thus, somewhat reduced oxygen levels would not necessarily have posed a significant challenge for the hypothesized Triassic Kraken, although we do not know precisely what type of cephalopod this creature represents. Nor do we known the size of the Triassic Kraken. Our estimate in the original abstract of 30 m is likely an overestimate; the attack on the ichthyosaurs could have been accomplished by a cephalopod approximately the same size as *Shonisaurus* judging from the Seattle Aquarium video of a Giant Pacific Octopus attacking a shark. Interestingly, the question of anoxic conditions versus aerobic conditions in the Holzmaden strata is still a topic of debate.

Regarding the question of sediment compaction, the process can certainly lead to “bed parallel alignment and more close-spaced packing” (Stow 2006). Compaction processes would tend to flatten the orientation of vertebral discs, especially if they rested on a relatively resistant, smooth hard surface. However, compaction processes do not appear to be capable of causing discs to move laterally to form an organized biserial array (Fig. 9.3). Furthermore, the ichthyosaur remains at BISP are preserved in a rather homogenous lime mud with no evidence for hardgrounds or other hard surfaces that could have served as a backstop for flattening the centra array by differential compaction.

A new development took place in the Triassic Kraken debate on January 5, 2013, when Thomas Dyer, the exhibits manager at the Nevada State Museum in Las Vegas (NSMLA), contacted me. He had been asked by Sali A. Underwood to forward to me photographs of a *Shonisaurus* fossil layout as presented as an exhibit at the NSMLA some decades earlier. The fossils were lain out as they had been discovered in the field at BISP. This contact with the NSMLA likely occurred because of the massive press attention that greeted the announcement of the Triassic Kraken hypothesis, and I am truly grateful to the science press community for having helped to initiate this contact.

The *Shonisaur* exhibit at NSMLA was fairly well known for the years that it was on display. At least one image of the exhibit had appeared in print in a geological publication. In an article in *California Geology* entitled "Ichthyosaurs of California, Nevada, and Oregon," Dupras (1988) published a photograph of the NSMLA exhibit with the following comment in the figure caption:

> Giant ichthyosaurs like *Shonisaurus* were extinct [by the Jurassic] and were replaced by smaller, swifter forms [paripelvians]. These remains were removed intact from the Ichthyosaur State Park and transported to the [NSMLA] for display.

Dyer (personal communication, 5 Jan 2013) was able to confirm that the bones in the exhibit were indeed laid out as found in the field, and that the intent was to "exhibit the fossil in the same relative positions as found." In addition to forwarding the photographs of the display, Dyer also sent two newspaper clippings describing the construction of the *Shonisaurus* exhibit.

The first of these (Anonymous 1980a) was published in the *Elko Daily Free Press*. The article reported that John Mawby of Deep Springs College, Bishop, California had been hired to construct the exhibit. The fossil bones were apparently stored in a garage at Washoe Lake, and were subsequently moved to the University of Nevada at Las Vegas. The article reports the interesting idea that the odd thickenings at the ends of the *Shonisaurus* ribs, not known in other ichthyosaurs according to Camp (1980), "may (or may not) have been for ballast." If for ballast, and the idea should not be dismissed out of hand, it would support the idea that these ichthyosaurs had an inherently positive buoyancy that needed to be compensated for by denser bone. If this was the case, shonisaurs might be expected to float some distance after death if they died near the sea surface under ordinary circumstances (Reisdorf et al. 2012, 2014).

Mawby went on to note the presence of presumed fetal ichthyosaurs in the rib cages of some of the female shonisaurs in the BISP region, and continued that they may "have become stranded on a mud bank" (a variant of the Camp stranding hypothesis). He also noted that they had very small brains and would thereby not be expected to have developed much of a "social impulse." Mawby reiterated that he planned to "assemble the animal in the position in which it was found." Mawby planned "only minor reconstruction, where adding plaster to the fossil will strengthen certain sections."

The second article (Anonymous 1980b) appeared in the *Nevada State Journal* of Reno. Describing the skeleton he was installing as the focus of the exhibit, Mawby said: "This is one of the most complete examples of the species [*Shonisaurus popularis*], and it gives the public a chance to see what was happening here in Nevada a couple of hundred million years ago." The article noted that the ichthyosaurs were marine and ate "small fish and squid-like cephalopods."

Figures 9.6, 9.7 and 9.8 are the photographs sent to me of Mawby's ichthyosaur exhibit at the Nevada State Museum in Las Vegas; Fig. 9.9 is my reconstructed

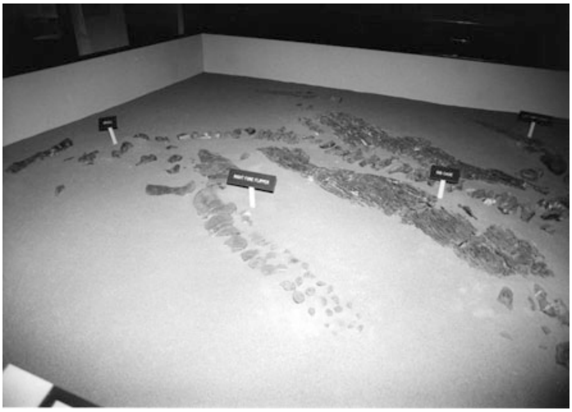

Fig. 9.6 *Shonisaurus popularis*. Bedding plane bone array formerly on display at the Nevada State Museum in Las Vegas (NSMLA). Front portion of reptile showing skull region, right fore flipper and rib cage. Photographer unknown

Fig. 9.7 *Shonisaurus popularis*. Bedding plane bone array formerly on display at the Nevada State Museum in Las Vegas (NSMLA). Posterior portion of reptile showing rib cage, right hind flipper, left hind flipper, and tail vertebrae. Note enigmatic bone cluster to the right of the rib cage, and the biserial arrangement of whole and broken vertebral centra in the right foreground. Photographer unknown

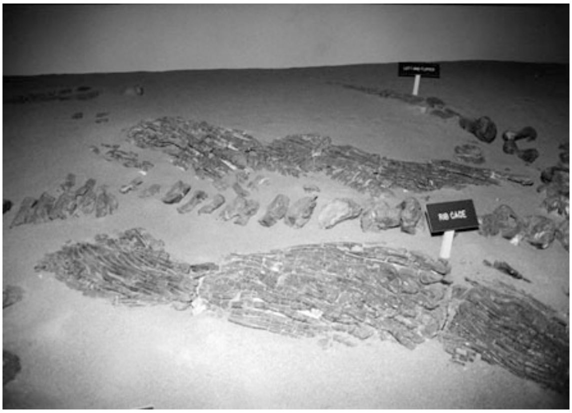

Fig. 9.8 *Shonisaurus popularis*. Bedding plane bone array formerly on display at the Nevada State Museum in Las Vegas (NSMLA). Detail of rib cage region showing enigmatic constrictions with breakage of the ribs. Photographer unknown

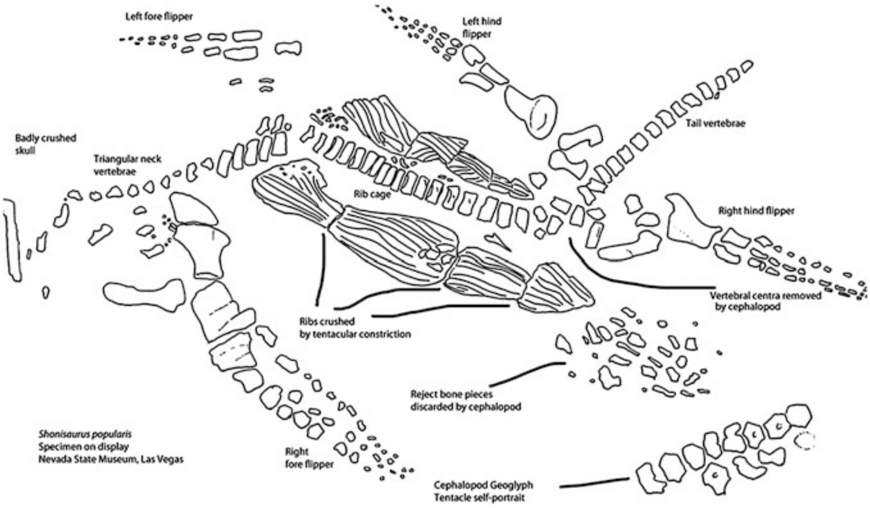

Fig. 9.9 *Shonisaurus popularis*. Bedding plane bone array formerly on display at the Nevada State Museum in Las Vegas (NSMLA). Sketch map of bone layout with interpretations of various regions of the skeleton

plan view map of the exhibit based on the photos sent and the photograph in Dupras (1988). The plan map is roughly accurate as it is based on photographs taken from a variety of perspectives on the exhibit.

Mawby built the exhibit in something resembling a giant concrete box form, with flat, presumably plywood panels enclosing the rectangular exhibit. The bones were set in a light-colored plaster or plaster-like compound. The matrix material was either sandy itself, or was dusted with sand while still wet to provide a natural ground-surface effect. Six sign panels mounted on flat sticks were pressed into the matrix to indicate the various parts of the *Shonisaurus* skeleton: “skull”, “right fore flipper”, “rib cage”, “right hind flipper”, “left hind flipper”, and “tail vertebrae”. There was an apparently longer text panel on the edge of the display (Figs. 9.7 and 9.8; you can just make out the edge of the display panel in the lower left of these two photographs) but unfortunately its text cannot be read in the photos.

The skeleton of the animal is indeed largely intact and does represent one of the most complete *Shonisaurus* specimens from Nevada. The left fore flipper is apparently present but lacked a label sign. The skull is fragmentary. The shonisaur was preserved lying on its back. Interestingly, a meter away and to the right of the mostly intact skeleton, additional vertebral remains are present. These form a pattern similar to Specimen U.

With its flippers splayed out to the side, and apparently the posterior half or so of the tail missing, the shonisaurs’ remains give the impression of a more plesiosaur-like body form (except lacking the long neck) than that of the canonical fish-lizard ichthyosaur body form as reconstructed by Camp (1980) and reproduced in Dupras (1988) beneath a photograph of the exhibit. With fore and hind paddles of comparable size, one gets the sense of quick up-and-down and torque/rotational manoeuvrability during forward motion, with the long tapered paddles serving an aileron or comparable type of elevator flight control function. Shonisaurs were thus water-fliers, the aces of the Triassic seas.

The skeleton and the vertebral centra nearby present a swarm of features that are difficult to explain. Most prominent are the strange constrictions and breakages to the rib cage of the main skeleton. These are visible on both the right and left sides as four or five subparallel constriction bands. The ribs have generally been displaced (squeezed?) to run approximately parallel to the backbone. The backbone has several kinks, one just anterior to the pelvis, one somewhat posterior to the shoulders, and a third apparently in the neck region. Two relatively well-preserved neural spines are visible just anterior of the posterior-to-shoulder kink. Vertebral centra appear to be missing from the spinal column in the vicinity of the pelvic kink.

A curious collection of bones, bone chips and fragments occur to the posterior right side of the rib cage. The material in this grouping seems to show a rough orientation, with some of the more elongate fragments oriented in a parallel fashion. This bone cluster is best seen in Fig. 9.7 and in the figure published in Dupras (1988, his “Photo 2”). Some of the bones in the bone cluster may be parts of ribs or the distally thickened ends of ribs (apparently unique to *Shonisaurus*; ribs in *Shonisaurus* are flattened near the spine and become thicker and more rounded in cross section away from the spine), but near the center of the cluster are two bones with polygonal outlines and dimpled centers that appear to be smaller vertebral centra. Several pieces on the left side of the cluster appear to be slivers taken from larger centra, complete with triangular notches taken off of the broken edges.

A second curious bone cluster occurs just anterior to the second right side rib constriction near the “rib cage” sign (Figs. 9.8 and 9.9). This appears to be a pile of rounded bones that looks like it has been stacked, and seems to include both a small centra and a teardrop-shaped (laterally flattened) possible caudal (tail) vertebra.

Finally, an array of twelve vertebral centra, forming a biserial array, is seen on the right side of the main skeleton just beyond the aligned bone cluster. Several of the centra in this array are intact and show the usual, roughly polygonal outline. Three or four of the centra are partial, generally half-centra, and along the broken edges there appear to be triangular notches removed from the bone (Fig. 9.7).

With the preliminary description of the exhibited shonisaur remains now complete, we may move on to the interpretation phase. It is a great pity that we do not have a published, complete description of the exhibit specimens by Camp himself; apparently he died before accomplishing this task. The rib constrictions probably represent the broken ribs that Camp (1980) does refer to in print. He attributed the breakage to “fighting” between the ichthyosaurs. The damage, however, does not seem to be of this nature. With fighting ichthyosaurs we would expect more localized rib breakage, where for example the beak of an attacking shonisaur pierced the side of its rival. In any case, the constricted, cracked ribs seen here would not be expected to occur by phytotoxin poisoning.

A better explanation is constriction of the shonisaur torso by some type of very powerful constricting band. The constricting grip of a very large serpent might accomplish this damage; however, snakes are unknown from the Triassic and in any case sea snakes kill by venom not constriction (and are not known to reach great size). More plausible is entanglement and squeezing by cephalopod tentacles of enormous size. Indeed, there seems to be little else that can plausibly explain the four or five bands of constriction as seen in the specimen. The force of the squeeze seems to have flattened the ribs to become parallel to the backbone.

Such a constricting force could also be responsible for the three kinks in the vertebral column. The missing vertebral centra in the vicinity of the pelvic kink may have been removed by the cephalopod. The two main kinks bend in opposite directions; they would bend to the same side of the animal if they represented current alignment. The impression here is of an unfortunate shonisaur that had the life crushed out of it by powerful tentacles applying constricting, crushing and torquing force from different directions as one might expect during cephalopod attack. Again, there seems to be no alternate way to explain the unusual post-mortem features seen in this skeleton.

The biserial centra array is interpreted here as a second cephalopod positive geoglyph, directly comparable to the Specimen U array of BISP. Rather than representing natural breakdown of a vertebral column, these geoglyph arrays were fabricated by the killer kraken, presumably to form patterns that matched the patterns of its tentacle suckers. The triangular chips taken out of the partial centra in the second geoglyph array may represent bite marks formed by the beak of the kraken. The bone cluster next to the rib cage may also be interpreted as a geoglyph, with the parallel nature of the elongate bone fragments having been arranged intentionally by the cephalopod.

An alternate explanation of the bone cluster is that it instead represents the gut contents of the stomach sack of the ichthyosaur that has protruded from the abdominal cavity (the bone cluster does not appear to represent fetal ichthyosaur bone material). This explanation, however, does not explain the oddly fragmented nature of the bone bits in the cluster. Shonisaurs did not have bone-crushing jaws or dentition, thus the bone cluster is not what one would expect to find in the stomach of *Shonisaurus*. Once again, the best explanation is organization of the roughly equal-sized bone bits by a cephalopod capable of segregating and organizing individual items by size and shape. Indeed, the second bone cluster is comparable to piles of shells arranged at octopus middens (Godfrey-Smith and Lawrence 2012). This type of cephalopod modification of the local environment has been identified as an example of ecosystem engineering (Scheel et al. 2014).

We see here a very interesting problem in marine reptile taphonomy whose best explanation, indeed the simplest explanation once all the evidence is considered, and thus an application of the principle of parsimony, involves a giant predatory cephalopod known as the Triassic Kraken. The kraken captured a large ichthyosaur, killed it with powerful tentacles, brought it to the sea floor, and was sufficiently intelligent to sort bone pieces by size and shape and arrange them into patterns or perhaps even create a self-portrait of the underside of one of its own tentacles. Also, if biting made the bone chips and triangular notches in the partial centra, this implies that the kraken had a very strong and powerful beak. The positive geoglyph is a pattern, possibly a copy of what the cephalopod saw when it looked at its own tentacle, but not necessarily what we humans would call a "self-portrait" nor evidence that the cephalopod was self-aware. Note, however, that informed researchers claim that it is time to recognize something in cephalopods that could rightly be called consciousness (Tennesen 1999; Anderson 2006; Montgomery 2015).

This would be a good time to rehearse some counterarguments. Let us say, for the sake of argument, that the shonisaurs were not killed by a giant kraken. In this case, the putative geoglyph arrays merely represent vertebral columns that have fallen apart as expected due to decay of soft tissue. Bone piles are merely odd clusters of bone. Some of the vertebral centra accidently clustered together in an approach to hexagonal closest packing. Due to the dense nature of the centra, more or less intact vertebral columns remained on the ancient sea floor long after the other parts of the skeleton have broken down, a phenomenon that is known to occur with cetacean remains.

Even if all of this were true, we would still be left with the fact that the ichthyosaurs were emplaced at different times. How could some skeletons be mostly intact, whereas others juxtaposed nearby are reduced to linear chains of centra representing the backbones? This represents a stumbling block for the phytotoxin poisoning hypothesis, as clusters of ichthyosaurs would be expected to have died at the same time. Furthermore, the deep-water emplacement and monospecific nature of the reptilian death assemblage are now well established. This poses further difficulty for the phytotoxicity hypothesis, as harmful algal blooms are associated with shallow water, and are known to simultaneously kill a variety of marine predatory animals. Only one marine reptile species is seen at BISP. Finally, the strange constriction bands and the apparent manipulation damage to the mostly intact skeleton shown in Figs. 9.6, 9.7, 9.8 and 9.9 would remain unexplained.

The kraken would have indeed required hard jaws as Seilacher pointed out, and we cannot dismiss the possibility that such were preserved. Bacterial degradation may be a problem, however; coprolite data indicate that coelacanth fish were in the area (McMenamin and Hussey 2015), but coelacanth bones and scales have otherwise not been reported from the Luning Formation and may have been lost to microbial breakdown. Our field excursions have recovered some tantalizing bits, but to date we have not recovered a convincing specimen of a large cephalopod beak from the Luning Formation. Cephalopod beaks are a rare fossil type; nevertheless, locating the beak of the Triassic Kraken may not be an impossible task. For example, a calcareous nodule from Wakkaweenbetsu Creek, Hokkaido, Japan has produced an enormous Cretaceous cephalopod upper jaw assigned (Tanabe et al. 2006) to the species *Yezoteuthis giganteus*.

Modern octopuses will kill sharks and use their beaks to pluck the flesh off the shark's remains, leaving behind a cartilaginous vertebral column that strongly resembles the long, relatively intact ichthyosaur vertebral columns seen at Berlin-Ichthyosaur State Park (McMenamin 2012). The best available explanation for the intact ichthyosaur vertebral columns is that they have been picked clean of flesh and surrounding bone. We see part of that process with bone bits apparently bitten out of the shonisaur body cavity (Fig. 9.7).

A possible argument against the Triassic Kraken hypothesis is the fact that the squid and octopus life span is so short, a few years at most. How could such short-lived creatures develop an artistic sensibility? In reply to this criticism, it might be said that very large shelled cephalopods of the past (*Cameroceras* and *Endoceras giganteum*, the largest nautiloids [6–9 m length], Teichert and Kummel 1960; Klug et al. 2015; *Parapuzosia*, the largest ammonite [3+ meters diameter]) must have had significant life spans in order to grow their gigantic shells. Triassic Kraken may be descended from one of these groups, and it is not implausible that it might have retained the ancestral longevity even if it did not retain the ancestral shell.

Also, a lives fast, grows big, dies young strategy for the Triassic Kraken is not out of the question either. Recall the Seattle aquarium video, where a captive Giant Pacific Octopus attacked and killed a dogfish shark. The octopus has a life span of 3–5 years, whereas the dogfish has an estimated life span of 25–100 years. The octopus killed a vertebrate that might have outlived its killer by a factor of 20–30. Octopuses evidently prey on and eat small sharks in the wild. A dogfish (*Squalus acanthias*) vertebral column, eaten clean like corn on the cob, was recovered in 2005 outside of an octopus (*Enteroctopus dofleini*) den (Onthank and Marsh 2005; Onthank et al. 2005). At the Fossil House quarry site, naked vertebral columns are the rule rather than the exception, suggesting that the shonisaurs were fed upon and partly disassembled (ribs separated from backbones) before the vertebral centra were rearranged. Long, isolated ribs also occur here, suggesting that they were pulled away from the backbone to which they were originally attached.

In conclusion, the Triassic Kraken hypothesis has survived all tests to date, including the current displacement probability test performed here, and is thus the leading explanation for the otherwise enigmatic arrangement of ichthyosaur bones at Berlin-Ichthyosaur State Park in Nevada. With octopuses herding crabs (Montgomery 2015) and carrying around empty coconut shell halves to use as defensive shields, and also to make clever, well-designed sheltering spaces (Finn et al. 2009), it appears that we have much to learn about the full extent of cephalopod behavior and intelligence both past and present.

Could an intelligent cephalopod make art, in other words, a geoglyph on the sea floor? It certainly seems possible, and may in fact be happening today. A 2015 survey account (Montgomery 2015) reports sea floor evidence for octopus activity consisting of “two crab claws piled on a flame scallop [*Lima scabra*] shell as carefully as a stack of plates piled in the kitchen sink after dinner… [shells] stacked up one atop the other, with the crab claws resting on top, like spoons in a bowl.” Could this in fact represent a crude pictograph of a crab, a landmark of some sort, or even a decoy to assist in crab herding? We do indeed have much more to learn. As Andrew Alden wrote in his October 14, 2011 article for *About.com.Geology* entitled “The Great Kraken Fracas”: “Why should we rule out intelligence in the distant past? And what would the signs of it be?”

As a final anecdote bearing on the Triassic Kraken hypothesis, consider an event that occurred on March 24, 2012 at the Ogden Point Breakwater in Victoria, British Columbia. Walking with family members along the breakwater, bird watcher Ginger Morneau noticed a seagull behaving oddly. She began snapping photographs of a

Fig. 9.10 Giant Pacific Octopus (*Enteroctopus dofleini*) showing arrangement of suckers on the underside of its tentacles. The sucker array closest to the photographer resembles the Specimen U array. Photograph by Mark McMenamin

Giant Pacific Octopus (*Enteroctopus dofleini*) attacking the gull, and holding its head underwater until it drowned. The entire predation event as recorded by the photos took all of 53 s. Morneau's still shots of the doomed bird went viral (many lament that she did not record the attack on video), and have added what would seem to be an improbable new item to the menu selections of Giant Pacific Octopus (Fig. 9.10). With birds representing the dinosaur clade, we can now say with certainty that an octopus is clever enough and strong enough to subdue and consume a small flying dinosaur (Sazima and Bastos de Almeida 2008; Nightingale 2012). Table 9.2 shows reports of birds attacked and killed by octopus ambush. Morneau's photographs imparted additional credibility to the earlier reports.

I hypothesize here that the octopus may ambush the bird by staying concealed in a, say, tide pool, while exposing the tip of one of its tentacles as a worm-like lure. There are curious reports, no longer easily dismissed, of large octopuses attacking and killing humans along seashores, including a report of a Native American woman who was bathing on the shore of Vancouver Island in 1877 before being

Table 9.2 Reports of octopus attacks on birds

Octopus predator	Avian prey	Locality	Date reported
Octopus n. sp.	Brown noddy (*Anous stolidus*)	West Atlantic island	2008
Giant Pacific Octopus (*Enteroctopus dofleini*)	Glaucous-winged gull (*Larus glaucescens*)	Victoria, British Columbia, Canada	2012
Giant Pacific Octopus (*Enteroctopus dofleini*)	Glaucous-winged gull (*Larus glaucescens*)	Whidbey Island, Washington, USA	2012
Giant Pacific Octopus (*Enteroctopus dofleini*)	Pigeon guillemot (*Cepphus columba*)	Whidbey Island, Washington, USA	2012

pulled down to an aqueous death, and of a Mr. Richard Shaw Burke who vanished on a rocky Tasmanian shore in 1913. Shaw's shirt was later found in the stomach of the largest Tasmanian octopus ever caught (Swancer 2014).

Allow me to propose a Triassic variant on the bird lure scenario, in a battle scene that I hypothesize took place beneath the Triassic waves. The Triassic Kraken coils up the tip of one tentacle to resemble a lively small ammonite or nautiloid. The lure has the proper color thanks to the magic of cephalopod chromophores, and moves up and down in the water in a thoroughly convincing manner. A *Shonisaurus* dives downward and observes what appears to be a proper prey item. Completely concealed in the dim light except for the coiled tip of its luring arm, the kraken emerges suddenly from its chromophore "cloaking device" and strikes as the reptile draws close. But instead of holding the reptile's head under water as in the case of the Glaucous-winged gull, the cephalopod impairs the ichthyosaur's ability to swim, stopping its ascent to the surface. The helpless flailing of the ichthyosaur, with kraken tentacles wrapped tightly around its trunk, another tentacle twisting its head to the right, and yet another pulling its tail to the left, only help to make the reptile run out of breath more quickly. After unceremoniously dropping the dead ichthyosaur upside down on the sea floor outside its lair, the Triassic Kraken returns to finish a geoglyph pattern nearby that it had been working on before the reptilian intruder transgressed into the kraken's realm.

Shonisaurs would have been badly outmatched by a large deep marine cephalopod, assuming that (as seems reasonable) the cephalopod had capabilities comparable to a modern octopus: superior vision at depth (detect differences in light polarization), camouflage (chromophores), superior strength (both radial and longitudinal muscle fibers), deadly tetrodotoxin (a potent neurotoxin), a self-awareness grade of intelligence, and an ability to respire frigid salt water. The only possible advantage that the shonisaurs might have had, besides their size, speed and pointy beaks, would be (possibly) color vision, although that is less useful in deep water where remaining light (aside from contributions due to bioluminescence) is mostly in the blue spectrum. Ichthyosaurs may have developed a very rudimentary version of echolocation, however, there is no convincing fossil evidence for this. The huge eyes of both pre- and post-Triassic ichthyosaurs strongly suggest a primary focus on vision.

An anecdote from an aquarist provides an example of the Triassic Kraken phenomenon in microcosm. A captive octopus repeatedly crawled out of its tank and into an adjacent aquarium tank, subdued twenty black tetras (*Gymnocorymbus ternetzi*), and returned them to its home tank, laying them out inside the conch shell it inhabited. The dead fish were not visible outside the tank, and the murderous theft was only discovered due to a nitrate spike detected in the octopus tank the next morning (Anonymous 2011).

There may be a better explanation than the Triassic Kraken for the features we observe associated with the marine reptiles of the Luning Formation, but I doubt it. Alternate explanations will require a mechanism for concentrating large ichthyosaur remains on the deep sea floor in the complete absence of evidence for funneling channels, submarine escarpments, etc. In scientific terms, this is a tall order. One might postulate that shonisaurs were so abundant that their remains littered the deep sea floor, literally piled on top of one another for thousands of square kilometers of seabed. The sedimentological evidence, however, indicates that shonisaurs were not nearly that abundant. The shonisaurs at BISP had been concentrated by some peculiar agency (Camp 1980). The burden of evidence has thus shifted to the kraken skeptics.

The taphonomy and arrangement of the *Shonisaurus* bones is truly strange. As Seilacher said, no other site is quite like this one. And as Laplace put it, the weight of the evidence should be proportioned to the strangeness of the facts. Available evidence strongly suggests that we are not looking at a simple case of soft tissue decay with associated passive disarticulation of the skeleton.

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Chapter 10
Dung Stones

In all things of nature there is something of the marvelous.
Aristotle, *Parts of Animals*

Abstract What did the giant *Shonisaurus* ichthyosaurs eat? Analysis of their coprolites indicates that shonisaurs fed on coelacanths, a fish type that is often associated with deeper water habitats. It is possible to make comparisons between Triassic and modern deep water, open ocean communities. Environmental convergence may be measured in *tetrapod:cephalopod:fish* trophic webs by means of the *corrected connectance* (C_c) parameter.

In our ongoing search to uncover fresh evidence bearing on the fate of the Berlin-Ichthyosaur State Park shonisaurs in the Fossil House quarry, our field excursion party recovered a Triassic crustacean fossil (Fig. 10.1) from a stream bed just to the east of the park boundary, where we were recovering numerous fossils of small clams, plus occasional ammonoids and nautiloids. It was clear that the fossil represented some type of malacostracan, and returning to the Paleontology Lab at Mount Holyoke, we undertook an effort to determine what type of creature it was.

I determined that the fossil represented some type of giant marine amphipod. This was exciting, because Mesozoic amphipod fossils are unknown, and the find promised to shed light on an important arthropod group that one might think should have an extensive fossil record going back to the Mesozoic and perhaps even the Paleozoic, but for reasons that are currently not well understood, the oldest amphipod fossils are only a few tens of millions of years old.

We described the fossil as the oldest known fossil amphipod, naming it *Rosagammarus minichiellus* after the student who had found the specimen (McMenamin et al. 2013). This appeared to be a major paleontological breakthrough, at least in terms of the Mofaotyof Principle. However, my colleague Thomas Hegna of Western Illinois University was skeptical of our claims and asked to examine the holotype specimen. After the fossil getting lost in the mail for some weeks, Hegna did finally receive the specimen as a museum loan. After some additional preparation of the fossil and examination of its surfaces under polarized light, Hegna concluded that instead of being the abdomen of an amphipod

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Fig. 10.1 *Rosagammarus minichiellus*, a Triassic malacostracan crustacean from the Luning Formation, Nevada; NCSM 11756. Scale bar in cm

malacostracan, it was part of the tail of a decapod malacostracan, something resembling a lobster or crab.

After reviewing the imagery and evidence, I eventually agreed with Hegna and his student that *Rosagammarus* was indeed a decapod not an amphipod (Starr et al. 2015). This serves as a cautionary tale concerning the dangers of attempting to interpret incomplete fossils. Nevertheless, the battle still goes to the bold. The species name *Rosagammarus minichiellus* stands in spite of the reassignment of the fossil to the decapods. It is much better for incomplete fossils to be named, as this brings more attention to the find and inspires debate and further field research. *Rosagammarus* remains an important advance in our understanding of the paleontology of the Luning Formation. Although arthropod fossils have been reported before from Triassic strata in this part of Nevada (Van Straelen 1936), they are poorly preserved or frustratingly incomplete. Everyone involved agrees that *Rosagammarus minichiellus* is the best arthropod fossil ever reported from the Luning Formation.

This is a good example of the self-correcting nature of scientific investigation. Further field study will hopefully uncover a more complete specimen of *Rosagammarus minichiellus*. Hegna and I would both like to examine the morphology of the *Rosagammarus* carapace to determine exactly what type of decapod it represents. And also, in spite of the temporary misidentification, it remains possible that, somewhere out there, perhaps even in the Luning Formation itself, a true Mesozoic amphipod awaits discovery.

Fig. 10.2 *Heteropolacopros* ichnosp., presumed juvenile *Shonisaurus* coprolite from the Shaly Limestone Member of the Luning Formation, just east of Berlin-Ichthyosaur State Park, Nevada, field sample 5 of 5/22/2014. Scale bar in mm

Undaunted in our search for more evidence bearing on the uncertainties surrounding *Shonisaurus*, we returned to the streambed area that yielded *Rosagammarus*. A Mount Holyoke College field excursion to the Upper Triassic Luning Formation in central Nevada in May 2014 yielded two coprolites derived from marine reptiles (Figs. 10.2, 10.3 and 10.4). The larger of the two is an odd, partly elliptical, dark-colored rock, while the smaller one resembles a tooth or even a stone bullet. Both specimens were recovered in float, the larger in the streambed at our main collecting site and the smaller specimen on a ridge on the north bank of the stream.

The stratigraphic position of the coprolites is in the Shaly Limestone Member of the Luning Formation, either in the Macrolobatus Zone or the underlying Schucherti Zone. Abundant specimens of small clams probably belonging to the genus *Septocardia* characterize both of these zones. The large coprolite was found in close association with numerous specimens of this clam, and thus its likely stratigraphic position within the Shaly Limestone Member is probably within the Macrolobatus Zone of the Late Carnian.

Both coprolites are flattened-ellipsoidal forms that are ellipsoidal in transverse cross section. A smooth rind of varying thickness constitutes the outer surface of each coprolite. A clot mottling texture occurs at places within the coprolite interior

Fig. 10.3 *Heteropolacopros* ichnosp., presumed adult *Shonisaurus* coprolite from the Shaly Limestone Member of the Luning Formation, just east of Berlin-Ichthyosaur State Park, Nevada, field sample 3 of 5/22/2014. This large coprolite is 9.2 by 5.8 cm in size, but is broken and part of the original coprolite was not preserved. Its original dimensions were approximately 16 cm by 9.5 cm. Collected by Mark McMenamin. Scale bar in cm

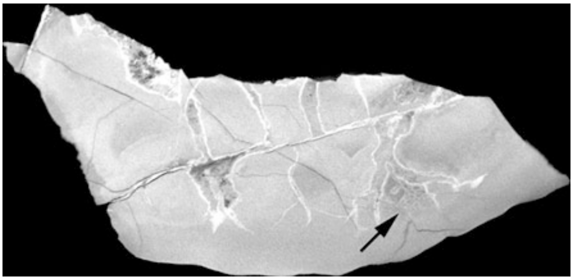

Fig. 10.4 *Heteropolacopros* ichnosp., CT scan of large coprolite in previous figure. Note polygonal internal fractures occurring in the interior of this large coprolite. Arrow indicates characteristic clot mottling on the interior of the coprolite. Greatest dimension of specimen 9.2 cm

(Figs. 9.4 and 9.5 in Chap. 9). The large specimen has faint latitudinal banding on the outer surface of the rind, but the coprolite does not have a spiral interior fabric. Both coprolites are assigned here to the ichnogenus *Heteropolacopros*, which is interesting, because this ichnogenus name has heretofore been used for terrestrial coprolites.

The smaller, bullet-shaped specimen (Figs. 10.2 and 10.5) collected by Nancy Hodge on the same expedition, that we at first thought was some sort of blunt tooth, was identified by Vince Schneider, Research Curator at the North Carolina Museum of Natural Sciences, as a coprolite. The larger specimen (Fig. 9.3 in Chap. 9) that I had collected had certain features (such as a rind-like outer coat) in common with the small specimen, leading me to suspect that both specimens were coprolites. A CT-scan at Hadland Laboratories in Amherst, New Hampshire confirmed that the large specimen had internal features (such as internal clot mottling) that were consistent with its interpretation as a large coprolite (Fig. 10.4).

Fig. 10.5 *Heteropolacopros* ichnosp., presumed juvenile *Shonisaurus* coprolite, detail of clot mottling visible on the surface of the coprolite. Width of photomicrograph 2.3 mm

Both coprolites have characteristics of Early Mesozoic reptile droppings (Hunt et al. 2013). Recall that one of the observations favoring the Triassic Kraken hypothesis is the fact that all of the skeletons in the ichthyosaur death assemblage belong to the same species. This led us directly to the reasonable inference that none other than Shonisaurus popularis produced the coprolites we had collected. We presented this conclusion at the Baltimore GSA meeting, along with an analysis of what we had found inside of the coprolite (McMenamin and Hussey 2015).

Ever since Mary Anning and William Buckland recognized that the fabled bezoar stones were coprolites (Buckland coined the term in 1829), these fossils have provided important paleoecological data. As interpretations of the Luning Formation paleoecology remain controversial, any new information regarding the paleoecology and diet of the *Shonisaurus* ichthyosaurs is potentially significant.

Ichthyosaurs first appear in the Lower Triassic with the appearance in eastern China (Motani et al. 2015) of *Cartorhyncus lenticarpus*. *Cartorhyncus* is already well-suited to an aquatic existence with its well-formed flippers. Its trunk and ribs resemble those of some early reptile-like tetrapods, thus it seems to have made the transition to mostly aquatic life early in the Mesozoic. By the Late Triassic, ichthyosaurs represent a tetrapod lineage that is still relatively new to the open marine environment. The shonisaurs and shastasaurs the size of whales suggests that these ichthyosaurs were thriving in their open ocean habitat. The *Shonisaurus* amphicoelous vertebral centra provide strong evidence that these animals were open sea, blue water creatures.

Modern whales are failures as producers of coprolites, because they defecate in a slurry that has essentially zero chance of being preserved in the rock record. To the delight of the ichnologist, ichthyosaur defecation was an entirely different matter. Land tetrapods of the Permian and Triassic often released feces hardened and condensed by inspissation, and ichthyosaurs are evidently descended from one of these compact mass-releasing tetrapod lineages. Ichthyosaurs retained this trait even after they became fully aquatic, retaining a water-retention adaptation developed by xeric landscape reptiles, and thus ensuring that Triassic and even Jurassic ichthyosaur coprolites would be available for study by paleontologists.

The lack of a spiral internal fabric to the coprolite indicates that these coprolites are not derived from sharks (Hunt et al. 2012). Elasmobranch coprolites have a spiral internal fabric. This is so because, as anyone who has dissected a dogfish will recall, sharks have a spiral lower intestine. Spiraling of the lower intestine allows greater surface area than a straight gut, and thus allows more complete absorption of nutrients from digestion. The ichthyosaur digestive system evidently lacked this intestinal coil, although we cannot by that fact alone infer that their digestion was less efficient than that of a shark.

A CT scan (Fig. 10.4) shows internal clot mottling in the large coprolite comparable to that of Late Triassic (Revueltian) inspissated coprolites from the terrestrial Bluewater Creek Formation, New Mexico (Hunt et al. 2013). CT scanning also reveals polygonal shrinkage fractures comparable to those of *Rhynchocopros soutoi* (Middle Triassic, Santa Maria Formation, Brazil). Very interestingly, bony fish remains are visible on a broken surface near the center of the large coprolite and at several other spots on the coprolite.

The smaller Luning Formation coprolite is 2.3 cm by 1.5 cm, with restored dimensions of 3 cm by 1.7 cm. Its small size suggests that it is derived from a juvenile animal. This coprolite also shows clot mottling (Fig. 10.5), exposed by breakage, at roughly the same interior position as seen in the larger specimen by means of the CT scan (Fig. 10.4).

Both coprolites are likely to have been produced by *Shonisaurus*, first because of their general similarity to early Mesozoic land coprolites belonging to the ichnogenus *Heteropolacopros*, and second, there are no other candidate reptiles known from the Luning Formation in the immediate vicinity of discovery or elsewhere nearby. Our field party searched for them with a Park Service vertebrate fossil-collecting permit in hand that would have allowed us to excavate a skeleton if necessary. We did not find any convincing evidence for other types (that is, non-*Shonisaurus* types) of marine reptiles. This does not mean that they were not present, but if they were, they were either much rarer than the shonisaurs, or more difficult to preserve as intact fossil bone, or both. In any case, the fact that the two coprolites we found were similar in shape, and could be assigned to the ichnogenus

Fig. 10.6 Coelacanth fish remains on the large coprolite. *Shonisaurus* large coprolite from the Shaly Limestone Member of the Luning Formation, just east of Berlin-Ichthyosaur State Park, Nevada, field sample 3 of 5/22/2014. Scale in mm

Heteropolacopros, renders it plausible that the coprolites were derived from shonisaurs at two different growth stages.

If so, and it seems likely at this point, these are the oldest known ichthyosaur coprolites, as well as the earliest known ichthyosaur coprolites reported from Nevada. The partially-digested fish bone in the larger coprolite provides direct evidence for the *Shonisaurus* diet, as described below. To summarize what we know at this point about the two coprolites: the overall fabric of the two coprolites (thick outer rind, internal clot mottling, flattened-tapered cylindrical shape) is strongly reminiscent of non-marine Triassic reptile coprolites, however, it is unlikely that true non-marine coprolites, even of the hard, inspissated variety, could have survived transport to the Luning Formation marine depositional environment. As noted above, it is more likely that the Luning Formation coprolites retain the general fabric of terrestrial coprolites because Triassic ichthyosaurs retained the alimentary and excretionary pattern of their land-dwelling tetrapod ancestors.

As noted earlier, fish remains are visible on the broken surface of the large coprolite (Fig. 10.6). These remains consist of relatively flat, roughly polygonal plate-like elements juxtaposed along suture lines (Fig. 10.7). A sinusoidal sagittal suture passes between the skull plates (Fig. 10.8). The remains therefore appear to represent the remains of a fish with a thick-plated skull.

Figure 10.9 shows a sketch diagram of the fish skull plates as visible on the broken surface of the large coprolite. As interpreted here, the fish skull remains retain two nasal plates, a pair of premaxillaries that would have housed the rostral organ, two tectal plates, three supraorbital plates and two frontal plates separated by the sinusoidal sagittal suture. The skull has been partly crushed or otherwise deformed,

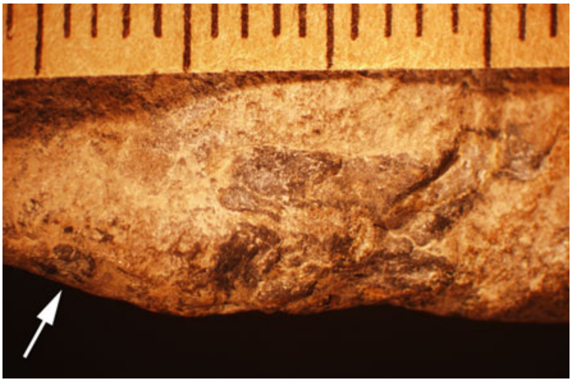

Fig. 10.7 Coelacanth remains consisting of relatively flat, roughly polygonal plate-like elements juxtaposed along suture lines. Premaxillaries are visible to the right (white arrow). Scale in mm

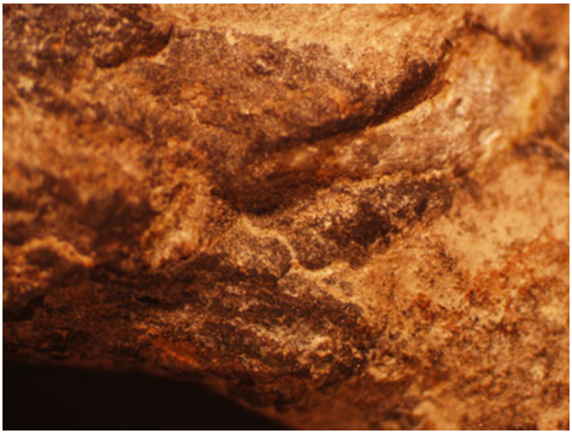

Fig. 10.8 Sinusoidal sagittal suture passes between the coelacanth skull plates. Width of view approximately 7 mm

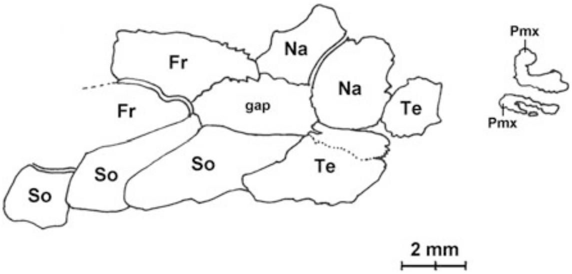

Fig. 10.9 Sketch diagram of the coelacanth skull plates as visible on the broken surface of the large coprolite. Scale bar = 2 mm

because a gap has opened up between several of the plates as seen in Fig. 10.9. The premaxillaries (Fig. 10.10) show evidence of vascularized bone in the form of obliquely positioned short hollow canals in the bone. They also show anterior openings for a rostral organ.

Fig. 10.10 Coelacanth premaxillaries. Width of view approximately 2.5 mm

With these observations on the fish material in the large coprolite, it becomes possible to make some inferences about the identity of the fish. Dense bone of this type would be one of the least digestible parts of the fish, and coelacanths are known to have thick skull plates at the tops of their skulls. Figure 10.11 shows a skull roof diagram (Forey 1981) of the coelacanth *Rhabdoderma*. Figure 10.12 shows a skull roof diagram for a whiteiidid coelacanth; it is morphologically more similar to the coprolite coelacanth than is *Rhabdoderma* because of its posteriorward-slanting supraorbitals (Fig. 10.12, arrows). The supraorbitals in the Nevada coelacanth are elongate and slant to the posterior rather than being roughly square to rectangular. The supraorbital configuration in the Nevada fish is thus closest to coelacanths belonging to the family Whiteiidae such as *Whiteia* (Nielsen 1936; Schaeffer 1952). Whiteiidid coelacanths are restricted to the Triassic.

A sinusoidal sagittal suture is shown in Fig. 10.11, and is very similar to that seen in the coprolite fish bone remains (Fig. 10.8). A rostral organ, as indicated by the coprolite-preserved premaxillaries, is unique to coelacanth fishes. The function of this zone in coelacanth fossils remained cryptic until a live coelacanth belonging to the genus *Latimeria* was discovered in the Indian Ocean in 1938. Subsequent analysis of these fish elucidated the nature of the rostral organ, presumably the coelacanth's chemosensory organ used for detecting prey. It is a fairly safe assumption that the rostral organ functioned in a similar way during the Mesozoic.

This is an exciting discovery from the interior of a coprolite. Ironically, the large coprolite has preserved the remains of a coelacanth that might otherwise be completely unknown to science as its bones or scales are not known from elsewhere in

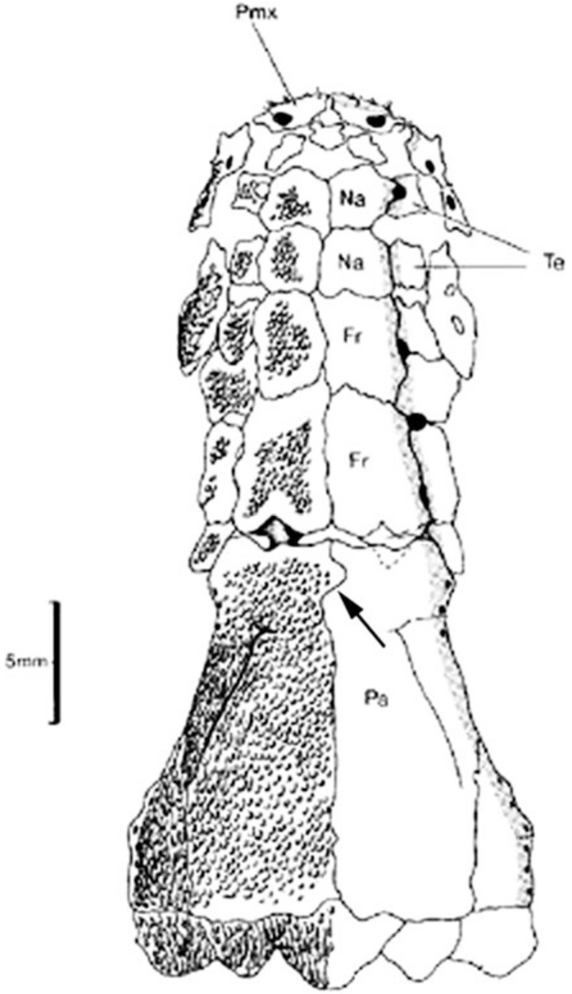

Fig. 10.11 Skull roof diagram of the coelacanth *Rhabdoderma elegans*. *Na* nasal, *Te* tectal, *Pmx* premaxillaries, *Fr* frontal, *Pa* "parietals". Note the sinusoidal sagittal suture (*arrow*) between the frontals and the "parietals". Scale bar = 5 mm. Redrafted from Forey (1981)

the Luning Formation. No coelacanth remains of any type have been reported from the Luning.

By a stroke of good fortune, the consumed remains of this prey fish are taxonomically informative—the coelacanth can be identified to the family level. Classification of coelacanths depends in large measure on the morphology of the skull roof plates. As noted earlier, the taxonomically critical skull roof plates of the coprolite fish are most similar to the those of the Triassic coelacanth family Whiteiidae. This comparison is based on similarities with regard to the posteriorward slant of the supraorbitals, which is apparently a distinctive characteristic for the Whiteiidae (Forey 1998). Thus, we can confidently claim that the ichthyosaur that created this coprolite (presumably *Shonisaurus*) was feeding on whiteiidid coelacanths.

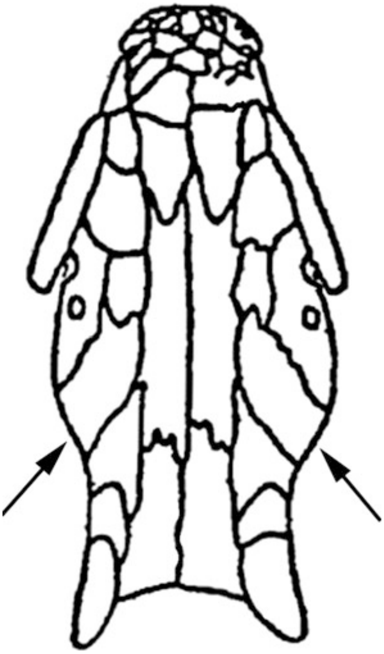

Fig. 10.12 Skull roof plates of a whiteiidid coelacanth, a group known to be restricted to the Triassic. Note posteriorward-slanting supraorbitals (*arrows*). Redrafted from Nielsen (1936)

In accord with this inference is the occurrence, also on the large coprolite of fragmentary and partly digested fish scale fragments that, although poorly preserved, are consistent with interpretation as coelacanth scales. A Triassic coelacanth scale, belonging to the coelacanth genus *Garnbergia*, was found in association with (but not inside) a giant Canadian ichthyosaur from the Pardonet Formation (Yabumoto and Newman 2004).

The discovery of these coelacanth bone (and possible scale) remains in the coprolite represents a huge step forward in understanding the paleoecology of the Luning Formation. In fact, it is better than finding coelacanth bones (even a more complete skeleton) in isolation because it gives us a link in the food chain. Furthermore, coelacanths are often associated with deep-water habitats, and this would be in accord with the emerging consensus on a deep-water interpretation of the depositional environment of the Shaly Limestone Member of the Luning Formation.

It is possible to take this analysis a step further. The modern deep marine ecosystem includes a triangular food web linkage (Fig. 10.13) of sperm whale (*Physeter macrocephalus*), colossal squid (*Mesonychoteuthis hamiltoni*), and patagonian toothfish (*Dissostichus eleginoides*). Note that both whale and squid feed on the toothfish. It is possible to speculate about a potential Triassic counterpart (Fig. 10.14) to the whale-toothfish-squid trophic triangle. In a prefiguration of the modern marine ecosystem, the trophic triangle in the Triassic may have

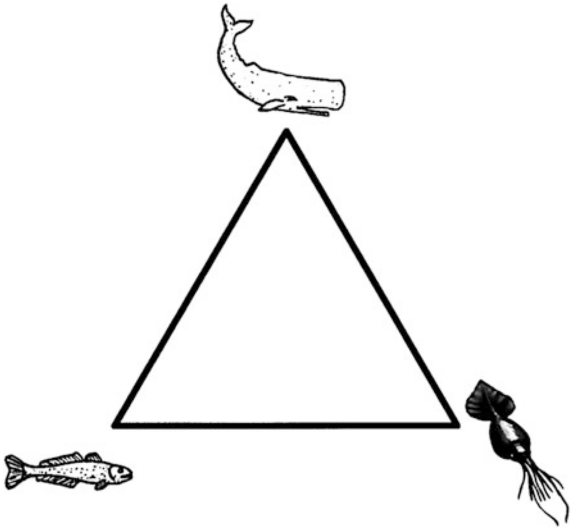

Fig. 10.13 Whale-toothfish-squid trophic triangle; a modern deep marine ecosystem triangular food web. *Artwork credit* Lower right, Citron/CC-BY-SA-3.0 [Creative Commons Attribution 3.0]

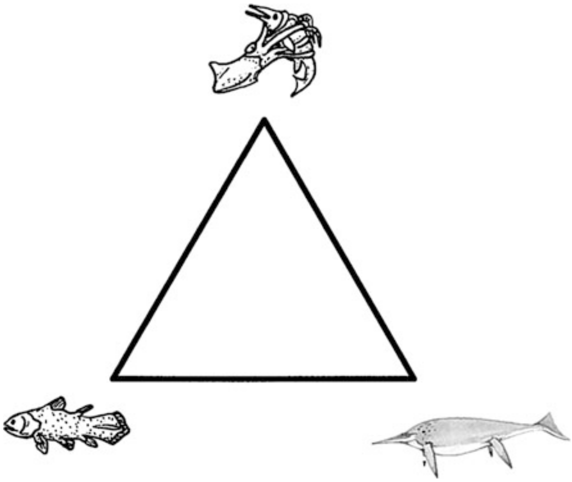

Fig. 10.14 Ichthyosaur-kraken-coelacanth Triassic trophic triangle. *Artwork credit* lower right, Dmitry Bogdanov [Creative Commons Attribution 3.0]

consisted of ichthyosaur-kraken-coelacanth, with the hypothesized Triassic Kraken at the top of an Early Mesozoic open marine trophic pyramid.

We can now confidently say that shonisaurs ate fish, and that the shonisaur diet included coelacanths. This inference, supported by several lines of fossil evidence, is consistent with a deep-water interpretation of the Luning Formation depositional

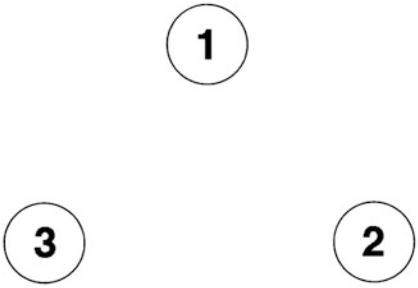

Fig. 10.15 Roopnarine (2010) diagram, food web consisting of species that do not interact. The hypothetical species are labeled *1*, *2* and *3*

environment. Today's triangular trophic web (whale-squid-toothfish) was prefigured in the Triassic as ichthyosaur-kraken-coelacanth. Thus, the post-Paleozoic open ocean can be considered as having repeatedly manifested the following generalized open ocean trophic web: large marine tetrapod; large cephalopod; deep marine predatory fish.

We can examine this further by means of food web, adjacency matrix and graph analysis (Roopnarine 2010). We will begin by introducing his four initial cases of simple graphical food webs. Each one of the four has a corresponding three-by-three adjacency matrix.

Figure 10.15 shows a food web consisting of species that do not interact. Its number of species or nodes, or verticies (n) is three. Its number of links or edges (|E|) is zero. Its adjacency matrix looks like this:

000
000
000

In an adjacency matrix, the rows and columns represent the nodes of the food web. If there is a link or edge between two of the nodes, then the value 1 is entered in two positions on the matrix. Consider Fig. 10.16. There is an edge or link between species 1 and species 3. Therefore the adjacency matrix for this food web is as follows:

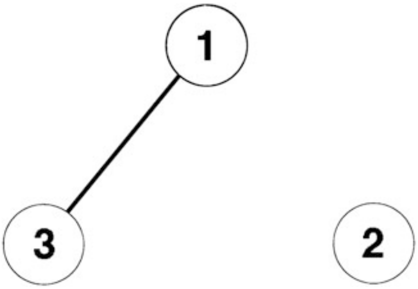

Fig. 10.16 Roopnarine (2010) diagram, food web consisting of three species with one interaction, link or edge

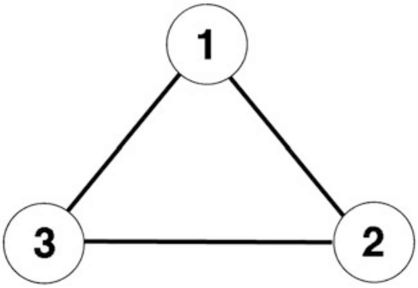

Fig. 10.17 Roopnarine (2010) diagram, food web with edges between all three nodes

001
000
100

In other words, species 1 interacts with species 3, producing a score of 1 in the upper right hand corner of the adjacency matrix, and species 3 interacts with species 1, producing a score of 1 in the lower left hand corner of the adjacency matrix. Note that two values are entered because the link is considered mathematically here to be bidirectional. Note, however, as Roopnarine (2010) put it, “Whereas the graphs illustrated so far have been *undirected* graphs, a [natural or true] food web is defined properly as a *directed* graph, or *digraph*. [italics his]”

Consider next a completed triangle, with edges between all three nodes (Fig. 10.17). This generates the following adjacency matrix:

011
101
110

Note in this adjacency matrix the line of zeros that slopes to the right along a 45° angle. These zeros indicate that the food web in Fig. 10.17 does not include cannibalism, or conspecific feeding. Figure 10.18 shows the food web when cannibalism is

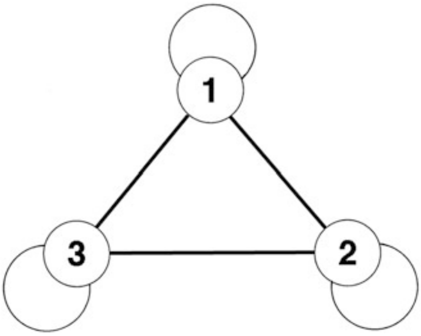

Fig. 10.18 Roopnarine (2010) diagram, food web with edges between all three nodes and cannibalism in all three species. The larger partial circle around each species indicates cannibalism within that species

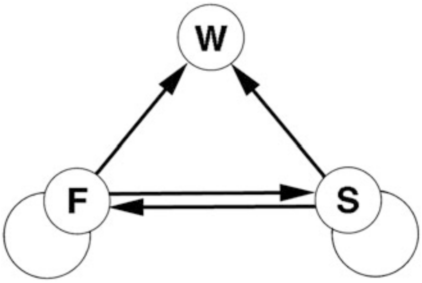

Fig. 10.19 Roopnarine (2010) diagram, modern deep marine ecosystem. *W* sperm whale; *S* giant squid; *F* patagonian toothfish

attributed to all three species. This then will generate an adjacency matrix that is completely full, as follows:

$$\begin{matrix}111\\111\\111\end{matrix}$$

Let's now apply Roopnarine (2010) analysis to real and hypothesized marine trophic webs. For this analysis we will need an additional parameter, L, the number of directional links in the food web. In the modern case (Fig. 10.19), we see that the sperm whale (*Physeter*) preys on both the patagonian toothfish and the colossal squid. Unlike ichthyosaurs, sperm whales are presumed to be able to stun their prey with a sonic blast after locating it via echolocation. The toothfish and the colossal squid prey on each other, hence that represents a bidirectional edge to the food web. There are four directional links shown in Fig. 10.19, therefore in this case L = 4.

Sperm whales are not known to be cannibalistic and therefore a simple node represents these whales. Cannibalism is assumed for the colossal squid, as cannibalistic behavior (Tennesen 2004) is well known in other cephalopods such as the Giant Humbolt or Jumbo Flying Squid (*Dosidiscus gigas*). Cannibalism has been confirmed in the patagonian toothfish (*Dissostichus mawsoni*; Arkhipin et al. 2003). This is indicated on the diagram.

Figure 10.20 shows Triassic case one, in which the Triassic Kraken is assumed to be both cannibalistic, and preyed upon (when young) by both coelacanths and

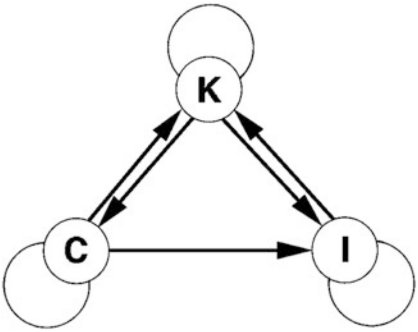

Fig. 10.20 Roopnarine (2010) diagram, Triassic case one, with Triassic Kraken cannibalism and predation on young krakens by coelacanths and *Shonisaurus*. *K* Triassic Kraken; *I Shonisaurus* ichthyosaur; *C* coelacanth

Shonisaurus. There are five directional food links in Fig. 10.20, giving a value of L = 5. We are assuming here that coelacanths did not prey upon ichthyosaurs. If the Triassic Kraken was cannibalistic, this would not be out of character for cephalopods large and small; the Giant Pacific Octopus will feed upon members of its own species.

Ichthyosaur cannibalism is well established by coprolites such as the Jurassic ichthyosaur coprolite *Ichthyosaurolites* (Hunt et al. 2012). Specimens of this coprolite ichnotaxon, including some from Buckland's original coprolite collection at Oxford, incorporate numerous skeletal remains of small ichthyosaurs. This does not of course demonstrate that shonisaurs were cannibalistic, but it is plausible that such behavior might have occurred.

The possibility of cannibalism in coelacanths has been widely discussed. The modern coelacanth *Latimeria* is piscivorous so it is plausible that an adult might feed on a juvenile coelacanth. A rancorous ichthyology debate took place over the hypothesis that *Latimeria* engaged in oophagy or embryonic cannibalism, but skepticism prevailed, and the current consensus view holds that the modern coelacanth does not in fact engage in intrauterine cannibalism (Heemstra and Campagno 1989), in other words, embryos eating their siblings while still inside their mother. The Roopnarine (2010) diagrams presented here all assume that Triassic coelacanths were indeed cannibalistic.

Figure 10.21 shows Triassic case two, in which the Triassic Kraken is assumed to be neither cannibalistic nor preyed upon at any point in its life cycle by coelacanths and shonisaurs. This might very well be the case if the hypothesized Triassic Kraken was intelligent enough to defend its young at all times, and neutralize threats such as predatory fish and marine reptiles. Three directional food links are shown in Fig. 10.21, giving a value of L = 3. The presumption in Fig. 10.21 is that coelacanths did not feed upon ichthyosaurs at any time.

We must now consider the concept of *connectance* as discussed by Roopnarine (2010). In graph connectance (C_g), the system describing mathematical food webs with edges but lacking directional food links, connectance is calculated as follows:

$$C_g = 2|E|/\left(n^2 - n\right) \tag{10.1}$$

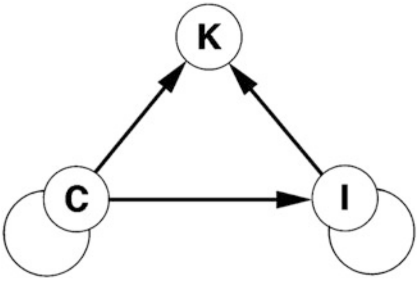

Fig. 10.21 Roopnarine (2010) diagram, Triassic case two, with no Triassic Kraken cannibalism and no predation on krakens by coelacanths and *Shonisaurus*. *K* Triassic Kraken; *I Shonisaurus* ichthyosaur; *C* coelacanth

For the graph shown in Fig. 10.17, with |E| = 3 and n = 3,

$$C_g = 2|E|/\left(n^2 - n\right) = 2(3)/(9 - 3) = 1 \tag{10.2}$$

For analysis of food web connectance, we must consider the number of directional links in the network (L). Thus, food web connectance (C_{fw}) of an actual marine food web is, according to Roopnarine:

$$C_{fw} = L/n^2 \tag{10.3}$$

The value of C_{fw} includes all links including with both directions of bidirectional links counted. For the modern food web (Fig. 10.19) with the whale as top carnivore:

$$C_{fw} = L/n^2 = 4/9 = 0.444 \tag{10.4}$$

The C_{fw} value for Triassic cases one and two would be 0.555 and 0.333, respectively. However, it is important to make a special accounting for cannibalism in nodal species, therefore I am defining here a new metric, *corrected connectance* (C_c). In order to calculate corrected connectance, we require an additional factor, the number of cannibalism links in the food web (B).

This modification to Eq. 10.3 is justified because members of the same species are born in cohorts, have similar or the same habitat and feeding preferences, may be as in the case of agnostid trilobites gregarious (as discussed in the next chapter), etc., and hence these are as important as interspecies links in the network and are thus given weight in the corrected connectance calculation. Corrected connectance is calculated as follows:

$$C_c = (L + B)/n^2 \tag{10.5}$$

In this new metric, instances of cannibalism factor into the connectance calculation. For the modern deep marine food web (Fig. 10.19), corrected connectance is:

$$C_c = (L + B)/n^2 = (4 + 2)/9 = 0.667 \tag{10.6}$$

Its corresponding adjacency matrix is as follows:

011
111
111

For Triassic case one (Fig. 10.20), corrected connectance is:

$$C_c = (L + B)/n^2 = (5 + 3)/9 = 0.889 \tag{10.7}$$

Its corresponding adjacency matrix is as follows:

111
111
111

Recall that this is the case where the Triassic Kraken is cannibalistic and is preyed upon by coelacanths and shonisaurs. For Triassic case two (Fig. 10.21), corrected connectance is:

$$C_c = (L + B)/n^2 = (3 + 2)/9 = 0.556 \tag{10.8}$$

Its corresponding adjacency matrix is as follows:

011
111
111

Recall that this is the case where the Triassic Kraken is not cannibalistic and is not preyed upon by coelacanths and shonisaurs. We can therefore come to a tentative conclusion regarding the structure of marine food webs. In a three node (three species) deep marine food web, corrected connectance values of $C_c < 0.7$ are consistent with dominance of the directional network links by an intelligent, K-selected predator (Reznick et al. 2002). Also, the adjacency matrix of the $C_c < 0.7$ state will take the following form:

011
111
111

In the modern (Fig. 10.19) and Triassic case two (Fig. 10.21) examples, this predator would be the sperm whale and the Triassic Kraken, respectively. We would not expect sperm whales to be cannibalistic, as they invest a lot of resources into relatively few offspring (in other words, they are K-selected). If Triassic case two is in fact the correct rendering of the Luning Formation deep marine trophic web, then we would expect the Triassic Kraken to be similarly K-selected, with extended care of its offspring as part of its behavioral repertoire (Kaneko et al. 2006).

Naked cephalopods do tend to have shorter life spans, as noted earlier. However, we must also consider the case of the deep marine octopus *Graneledone boreopacifica*. A mother belonging to this species has been recorded tending a single clutch of 160 eggs for an amazing four and a half years. This record-breaking nest sit occurred at a depth of 1397 meters at the base of the submarine Monterey Canyon (Robison et al. 2014). According to Brad Seibel of the University of Rhode Island (Netburn 2016): “This is the longest brooding or gestation of any animal on the planet.” This surely qualifies as a variant of K-selective behavior, thus the concept of similarly K-selected deep marine Triassic cephalopod is quite plausible.

With the corrected connectance metric in hand we have taken a first step toward quantifying the similarities between food webs, of different geological eras but of comparable structure due to environmental convergence. In other worlds, in networks with n = 3, corrected connectance drops below values of 0.7 as the intelligent predator emerges. Also, the adjacency matrix in these cases acquires the following values:

$$\begin{matrix}011\\111\\111\end{matrix}$$

This method of analysis holds promise for more complicated trophic webs as well. In any such attempt, I recommend that the analysis focus more on corrected connectance and its permutations rather than on what is called the coordination number of the graph, in other words, the average number of links per species (z). Poisson distributions with mean z form graphs known as Erdös-Renyi graphs. According to Roopnarine (2010), Erdös-Renyi graphs “possess many interesting properties [although they] rarely describe real-world food webs.” Food web connectance (C_{fw}) values are typically used to show increases in link density as they rise with increases in species richness. Roopnarine (2010) notes that it “is possible that increasing taxon richness in a community demands greater connectivity in order to maintain efficient energy transfer and hence stability, or the relationship is simply spurious and any true relationship is obscured by the heterogeneity of food web metadata. This remains an open problem in food web data.” Analysis of the same data by means of corrected connectance will put the appropriate weight on intraspecies trophic interactions, and this has potentially profound implications for the structure of the marine biosphere as we will see in the case of Cambrian agnostids.

As was the case for Proterozoic marine and Mesozoic lacustrine microbial mat-dominated environments and their intriguing occurrence at separated moments in geological time by means of environmental convergence, we see with the *tetrapod:cephalopod:fish* triangle another environmental-ecological convergence that this time links the Mesozoic with the Recent.

This critical discovery points to undiscovered laws of environmental evolution (McMenamin 2001), an environmental *Nomogenesis* in the sense used by Berg (1969), who advocated for laws involving homoplasy and convergence as applied to biological evolution. We have reached in interesting juncture. It is now appropriate to say that we inhabit a law-governed universe, at least as far as we can take our dynamic analysis of the evolution of complex life forms and the evolution of the environments in which they live or lived.

This analysis points an accusing finger right at the sensitive spot in the contemporary "received wisdom" concerning the validity of conventional, gradualistic Darwinian evolution. Using the corrected connectance metric, we can now make quantitative predictions about how ecosystems will appear. There does seem to be a certain inevitability to the appearance of networks with particular properties as a result of the playing out of natural law as applied to the evolution of the biosphere.

This is not to say that natural selection does not occur. It does, continuously, and it certainly influences the evolutionary changes that creatures experience through time. But to emphasize the supposedly random aspect of natural selection, as an excuse to deny the reality of universal or natural law, flies in the face of the evidence presented here showing that the world is governed by discernable laws that can be discovered by dynamic analysis of patterns in nature that are manifested through time.

Before bidding the shonisaurs of Berlin-Ichthyosaur State Park *adieu*, and returning to the Cambrian, I ask your assistance esteemed reader for help in tracking down both the source and basis in truth of a rumor regarding a lost *Shonisaurus* skeleton. I almost never mention rumors in print, and this particular rumor does not quite rise to the level of infamy attached to the lost Peking Man fossils (Aczel 2008). However, the importance of this putative lost skeleton (assuming it exists) is of potentially greater importance if it can shed additional light on the (now critically important for paleontology) Triassic Kraken hypothesis.

This rumor of a lost skeleton was told to me on May 27, 2014 by Jack Desai, Owner of America's Best Inn and Suites, Hawthorne, Nevada. This hotel was built in 1991. In 1992, according to Desai, four British paleontologists stayed 3–4 months and excavated a sixty-foot long "whale" and boxed it in 4 sections, and sent it to a museum in Britain, possibly the British Museum. The excavation was near Gabbs, Nevada. The paleontologists were very excited about this find, presumably a shonisaur or other large ichthyosaur. Desai said that a video was made of the excavation, but he was unable to locate his copy while I was staying at his hotel in Nevada. If anyone reading this book can confirm (or repudiate) this rumor, particularly if you have any information regarding the (possibly unauthorized?) excavation and especially the current location of the skeleton, please contact me immediately.

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Chapter 11
Cambrian Cannibals

Certainly, let us learn proving, but also let us learn guessing.
George Pólya (1887–1985)

Abstract What role did agnostid trilobites play in the Cambrian ecosystem? Agnostids were predatory, and were capable of killing smaller members of their own species. Genocide and cannibalism can be traced back to the Early Cambrian, as can cooperative behavior such as group migration. It is plausible to predict that eusociality (at least in its rudimentary sub-social form) will eventually be discovered in the Lower Cambrian fossils record, as an aspect of the abrupt nature of the Cambrian Explosion.

The Early Cambrian witnessed the appearance of the first large swimming predators, the fearsome (at least from the perspective of typical trilobites) anomalocaridids of the Family Anomalocarididae. The largest of these creatures (*Anomalocaris canadensis*) reached over a meter in length. They were evidently able to capture and consume prey by means of a circular mouth that resembled a pineapple ring and two hook-like appendages. More importantly, they located their prey by means of the most advanced eyes of their day. Estimates of anomalocaridid vision suggest an impressive acuity. Each anomalocarid eye consisted of 16,000 lenses, comparable to the modern dragonfly eye (28,000 lenses per eye), and the two may have had comparable degrees of resolution. Patterson et al. (2011) write that:

> The inferred acuity of the anomalocaridid eye is consistent with other evidence that these animals were highly mobile visual predators in the water column. The existence of large, macrophagous nektonic predators possessing sharp vision—such as *Anomalocaris*—within the Early Cambrian ecosystem probably helped to accelerate the escalatory 'arms race' that began over a half a billion years ago.

The concept of a Cambrian arms race echoes a general sentiment in paleontology that has been around for over a century since philosopher Henri Bergson first articulated the idea (McMenamin 1998). The image of a link in terms of visual acuity between anomalocaridids and dragonflies is amusing and instructive.

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Springer Geology, DOI 10.1007/978-3-319-22777-1_11

A dragonfly can be viewed, in a sense, as a pair of flying *Anomalocaris* eyes, with a pencil-thin minimalist body and grasping appendages to snatch insects out of the air.

A large animal with the ability to seek out and capture prey using an acute visual system surely must have influenced the evolutionary dynamics of the Cambrian Explosion. These dynamics rapidly veered off into some interesting directions. For example, a maverick group of anomalocaridids belonging to the genus *Tamisiocaris* represent an offshoot in which the great appendages, used in normal anomalocaridids to draw prey into the circlet mouth, have been modified into sieves consisting of a main branch with numerous fine branchlets, each itself bearing fine spines, forming a mesh structure that has been compared to baleen in modern whales. In a video that accompanies the description of the genus (Vinther et al. 2014), *Tamisiocaris* is styled as the "gentle giant of the Cambrian."

Tamisiocaris itself provides further insight into the feeding of the typical anomalocaridids. Hagadorn et al. (2010), using finite element analysis, have argued that the typical anomalocaridids did not have a mouth strong enough to bite through the tough trilobite carapace. Hagadorn et al. (2010) note that a "rapidly closing anomalocaridid mouth could generate sufficient external pressure change to allow suctorial feeding—yet no anomalocaridid mouth could close more than half-way."

At first I was very skeptical of the Hagadorn et al. (2010) hypothesis, and I pointed out in a report on the "shrimp from hell" that we must somehow account for damage seen on numerous specimens of otherwise ordinary Cambrian trilobite fossils (Anonymous 2013).

> The damage to those Cambrian trilobites is real, and if it was not *Anomalocaris's* doing, who then was the predator? If Hagadorn is right and *Anomalocaris* could only gum its prey, then the search is on for the actual durophagous (that is, shell-cracking) Cambrian predator.

Fundamentally, however, Hagadorn et al. (2010) make an excellent point. Anomalocaridid feeding makes more sense if their two anterior great appendages were used to hold their prey against the pineapple ring mouth, which then by grinding, suction or some other method would consume the prey item. If *Anomalocaris* pressed the prey item to the circlet mouth by means of its appendages, its secondary branches would help to hold the prey item in place. The food itself could provide the seal to allow sufficient suction to occur. This very method of feeding could be fairly easily adapted to filter feeding. One can easily imaging a hungry anomalocaridid making an inefficient but successful attempt at filter feeding in a thick swarm of plankton by sweeping small floating or swimming larvae into its mouth by means of its great appendages.

Curiously, the concept of a filter-feeding anomalocaridid did not originate with discovery of the critical fossil remains in Greenland (Daley and Peel 2010). Well before the description of *Tamisiocaris*, artist John Meszaros painted a concept art piece of an imaginary creature that showed Meszaros's concept of an anomalocaridid that had developed into a gentle filter-feeding giant comparable to baleen whales and whale sharks. Meszaros explained (Wason 2015):

> My animals are speculative, but they might have existed, or something like them may have existed—we just haven't found the fossils for them yet… There's a huge gap of time where there's not really any evidence [for filter-feeding animals of this nature]… So I was trying to think what sort of creature could fit that niche, and I thought anomalocaridids would be perfect.

Meszaros's artist's intuition was accurate, and there certainly are additional paleoecological niches filled by organisms that have not yet been recovered as fossils. A larger point emerges from this art-in-paleontology coup, however. The appearance in the Early Cambrian of an anomalocaridid filter-feeder underscores once again the abrupt nature of the Cambrian Explosion. That an anticipated ecological type turns up so early in the Cambrian testifies both to the rapid occupation of available niches and to the unusually un-gradual dynamics of evolutionary change during the Explosion.

We can pursue this a step further, and ask: What other types of ecological interaction and/or trophic and behavioral interactions might we expect during the Cambrian Explosion? Trilobites, possibly a preferred prey item for anomalocaridids (especially if they were freshly molted and hence soft-shelled), were themselves predators in many cases. The underside of trilobites is often considered to be their weak point, a soft underbelly that was far more vulnerable to attack than their mineralized upper carapace.

In some trilobite species, however, the appendages under the carapace could deliver a nasty pinch or worse. Paired gnathobases, positioned at the bases of each set of biramous appendages (trilobites have a gill branch associated with each walking leg), would have a comparatively powerful pinching force due to short-blade mechanical advantage as is the case for a pair of bolt cutters. For example, the trilobite *Olenoides* was armored with spiny gnathobases at the base of each pair of legs. The spines projected inward toward the animal's underside midline. When brought together, the gnathobases were capable of driving sharp spines through the integument of an intended prey item such as a soft-bodied priapulid worm.

The damage inflicted would be traumatic and extensive, because each base of the many pairs of legs carried the deadly gnathobase spikes. The gnathobases would be able to move back and forth with a shredding action. This nearly instantaneous shredding of the prey would accord with the typical mode of trilobite feeding, whereby particulate food from the sea floor is put into suspension by leg action and then vacuumed up by the backward-pointing trilobite mouth known as the hypostome complex.

The oldest evidence for predation in the fossil record is a curious arcuate bite or slice taken out of the side of the approximately 750 million-year-old vase shaped microfossil *Bonniea pytinaia* (Porter 2004). This "semicircular hole" is small, only about 17 microns in greatest dimension. The oldest evidence for predation in animals is a combination trace fossil from the lowermost Cambrian unit 3 of the La Ciénega Formation in Sonora, México (McMenamin 2003). The predator in this case is thought to be an early trilobite, possibly a fallotaspidoid trilobite. The specimen shows a curving trackway (ichnogenus *Planolites*) intersected by a trilobite trace fossil assigned to the ichnospecies *Rusophycus multilineatus*. Although based on a single specimen, analysis of later instances of possible predation in associations (Tarhan et al. 2011) of trilobite *Rusophycus* traces and various types of "worm burrows" (*Palaeophycus*, *Planolites*, *Teichichnus*, *Gyrolithes*, and *Helminthopsis*) have added additional credence to the Sonoran example of a very early predation event (McMenamin 2011).

In a recent study of trilobite ichnofossils, Selly et al. (2016) conclude:

> *Rusophycus* traces intersect vermiform burrows more often that expected by random chance and display a positive correlation in size between paired tracemakers. The median diameter of *Rusophycus*-associated vermiform burrows is significantly smaller than that of the non-intersected burrows. These results suggest that the paired traces record size selective predatory behavior.

Trilobites were evidently selecting the small vermiforms, presumably because they were easier to subdue. Larger trilobites would tackle larger worms. The statement that trilobites were predatory, and that they preyed on a variety of vermiform creatures of the Paleozoic sea floor, is now firmly established by multiple studies. Note carefully that I used the phrase "firmly established," not the word "proven." Other interpretations of available trilobite ichnofossil data are still possible, although alternative explanations at this point seem much less likely.

Agnostid trilobites, like so many other animal types, appear first in the Early Cambrian. Adult agnostids are tiny compared to their better-known, larger relatives. Agnostids survived for almost exactly one hundred million years, appearing in the Early Cambrian (542 million years ago) and surviving until end of the Ordovician Period, about 443 million years ago. Largely due to their diminutive size, agnostid trilobites have defied attempts to properly interpret their affinities, environmental preferences, behaviors and feeding strategies (McMenamin 2010). It is however clear, as one might expect considering their small size, that agnostids served as prey items during the Cambrian. Zhu et al. (2004) reported the remains of the Middle Cambrian eodiscoid agnostid trilobite *Pagetia* preserved in what they interpreted as the serial digestive glands of a large predatory arthropod allied to Lower Cambrian *Fuxianhuia*.

Results from a suite of 44 separate slabs bearing specimens of the Cambrian agnostid *Peronopsis interstricta* have provided new data concerning agnostid behavior. Most of the specimens (n = 43) were donated to Mount Holyoke College by an alumna, so their precise fossil locality is unknown. Nevertheless, the samples are most likely derived from the Middle Cambrian Wheeler Formation, Millard County, Utah. An additional slab, also derived from the Wheeler Formation in Millard County, was purchased for comparison purposes. The matrix of the purchased sample shows iron staining that does not occur in the donated samples, thus the suite of samples probably represents at least two separate stratigraphic horizons within the Wheeler Formation.

Seven samples out of the entire original (donated) suite (16 %) contain juxtapositions of large (>4 mm) and small (<4 mm) specimens. In cases of what I consider to be Cambrian versions of *Duria Antiquior*, the small individuals of the pairs frequently appear to be damaged (Fig. 1). In some cases a small individual is

Fig. 1 Cambrian agnostids belonging to the species *Peronopsis interstricta*, with possible attack of the larger trilobite upon the smaller in what is interpreted here as an early instance of arthropod cannibalism. Scale in cm

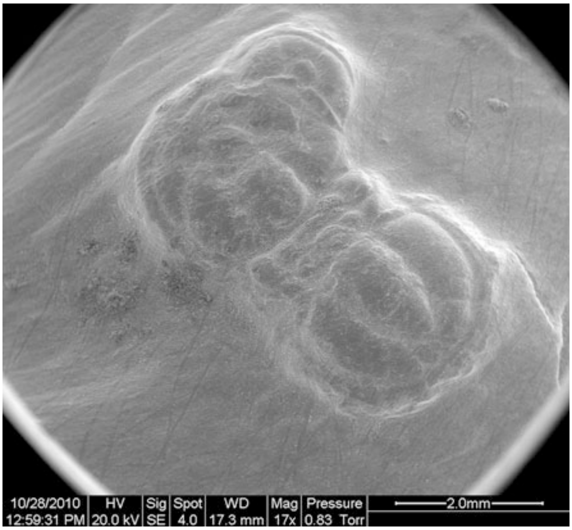

Fig. 2 *Peronopsis interstricta*, SEM micrograph. This slab shows a small individual overridden by the cephalon of a larger animal. Scale in mm

overridden by the cephalon of a larger animal, in what does not appear to be a merely chance association (Fig. 2). I interpret these associations as evidence of attack by the larger member of the conspecific pair (McMenamin 2012). Of the samples preserving multiple trilobites, 58 % show evidence for cannibalism.

These results suggest that *Peronopsis interstricta* was a predator. The predator inference is supported by putative tiny bite scars on the pygidium of a specimen of *Peronopsis interstricta*, damage that likely is the result of intraspecific attack (Babcock 2003). The damage looks like someone nicked the posterior edge of an agnostid with a manual hole puncher.

An alternative to the predatory attack interpretation might be that the attacks represent an expression of intraspecific territoriality or mating behavior. Scavenging and accidental juxtaposition scenarios must also be considered. A cannibalism explanation, however, seems best supported by the available data. If so, these encounters represent the earliest known examples of arthropod cannibalism, and thus add to the accumulating evidence indicating that the Cambrian biosphere experienced a bizarre and unprecedented increase in marine predation pressure. Furthermore, cannibalism might also be considered as a potential accelerating or contributing factor to the appearance of widespread Cambrian predators.

As the agnostid *Peronopsis interstricta* was evidently blind, these predatory trilobites must have relied on senses other than sight to locate and capture their prey. Alternate sensory modalities, such as chemotaxis, electrotaxis or phonotaxis, may have been utilized in a search for prey. Several of the slabs may be arranged in such a way to suggest that the attacking trilobite approached its smaller prey in a coiling trajectory, spiraling inward to eventually seize its hapless victim (Fig. 3).

Other interpretations of the seek-and-destroy pattern are also possible. We might be able to obtain an unambiguous solution to the approach pattern problem if a slab were to be located that shown agnostid trace fossils (fodichnial traces) associated with the body fossils. Unfortunately, such associations of body fossils and ichnofossils are very rare in Cambrian rocks.

The earliest known case of cannibalism of all time, just slightly older than the case for agnostid cannibalism (but still Middle Cambrian), occurs in fossils of the Burgess Shale priapulid worm *Ottoia* (Nudds and Seldon 2008). A number of

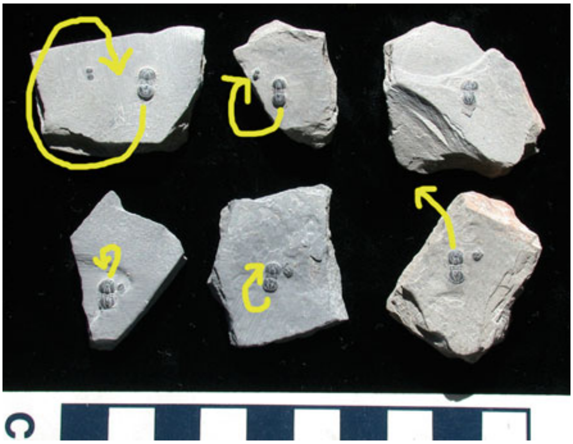

Fig. 3 Attacking trilobite approached its smaller prey in a coiling trajectory, spiraling inward to eventually seize its hapless victim. *Top left* larger trilobite begins to spiral in towards small trilobite; *top middle* large trilobite spirals in closer; *top right* large trilobite attacks smaller; *bottom left* large trilobite moves away from cannibal feast remains and turns left; *bottom middle* large trilobite turns right; *bottom right* large trilobite veers left and leaves the scene of the cannibal attack. Scale in cm

specimens are known in which a large *Ottoia* has swallowed a smaller *Ottoia* of the same species. Cannibalism is commonly seen in modern priapulid worms. No cases of cannibalism have been reported yet from the Early Cambrian; however, this is likely to be a sampling artifact as per the Lignor-Sipps Effect (McMenamin 2014). The trace fossil *Treptichnus pedum* may represent the ichnofossil of an early priapulid worm. If so, this Early Cambrian tracemaker was likely cannibalistic as well.

Interestingly, both the priapulid *Ottoia* and the agnostid *Peronopsis* were apparently blind. This implies that cases of early cannibalism are not necessarily associated with vision-directed predation. Especially since the discovery and interpretation of complete anomalocaridid fossils, vision-directed predation has been blamed as the primary trigger for the development of skeletons during the Cambrian Explosion (McMenamin and Schulte McMenamin 1990).

Ecological reconstructions of the Cambrian sea floor should now portray agnostid trilobites as predators. The agnostid species *Agnostus pisciformis* had antennae with regularly placed spikes that may have served a predatory function, in the same way that spiny gnathobases allowed larger trilobites to attack their prey. Cannibalism should thus be considered a potential contributing factor to the appearance of widespread Cambrian predators. The behavioral tools associated with macropredation may have been first refined within a single species before being unleashed on the rest of the marine biosphere. This might have been the case, for example, for a biomat grazing animal or undermat miner that made use of sensory input data to locate mates in, say, a tenebrous sub-biomat film habitat. In some modern arthropod species, such as the widow spiders (*Lactrodectus* sp.), cannibalism is closely associated with mating and this association may be very ancient. If sensory refinement allowed the early biomat animals to locate eligible members of the opposite sex, then further refinement of these same senses could easily lead to an ability to distinguish nearest of kin from more distant relatives in the same species.

The small agnostids that appear to have been killed by members of their own species often do not show clear evidence of having been eaten by the larger agnostid. I propose here that the agnostid attacks were not predatory cannibalism, but rather that the larger trilobite was able to sense that the smaller trilobite did not belong to the same tribe, and therefore was targeted for death. If this interpretation is correct, this then represents the first known instance of genocide.

The hypothesis would be difficult to test, although it is possible that racial markers (morphological or even geochemical) could be detected that would allow us to discern the various races of *Peronopsis interstricta*. If we assume (as seems likely) that the small agnostids are younger than the larger specimens, then we would also see here the earliest known example in the biosphere of infanticide. But rather than being filial infanticide, where parents kill their own offspring, the case of *Peronopsis interstricta* may indeed represent genocide: a racially-motivated attack where very acute sensory cues indicate to the attacking adult that the juvenile is the member of another lineage or tribe. This case would then be the original racism, where kin recognition acquired a dark and deadly aspect. There is no doubt microbial precedent for this antagonism between, say, different microbial strains

(Hibbing et al. 2010), but this discovery represents its first appearance in complex multicellular organisms.

A piece of evidence in favor of this hypothesized race-based infanticide is that *Peronopsis interstricta* fossils are commonly found in conspecific groups or packs. These may represent cohorts of closely related, gregarious individuals. Also, the juvenile agnostids appear to be merely split in half along the zones of weakness associated with the two pleural segments of the agnostid thorax. This was probably accomplished by a gnathobase-like action from the appendages of the adult *Peronopsis*. The adult did not seem to make any effort to ingest the juvenile, although we cannot rule out some type of suctorial feeding as inferred above for the anomalocaridids.

Infanticide has been recorded from invertebrates such as rotifers and insects, and in vertebrates such as fish, amphibians, dinosaurs (including of course birds) and mammals. The Cambrian also records the origin in animals of collective and apparently cooperative behavior. Hou et al. (2008) have reported from the Early Cambrian Chengjiang Lagerstätte a previously unknown arthropod that formed conspecific caravans. Hou et al. (2008) report: “The chainlike form of these specimens is unique for any arthropod, fossil or living, and most likely represents behavior associated with migration.” This is not strictly true, as chains of trilobites are known from the Holy Cross Mountains in Poland. But once again, we see an unusually early ‘advanced’ behavior. As with so many aspects of animal life, the trail leads back to the Early Cambrian.

The research presented here on microburrow nests and agnostid trilobites leads to an important prediction. In accord with the by now familiar pattern of finding virtually all of the most ‘advanced’ aspects of animal evolution to have originated in the Early Cambrian, it is only a matter of time before a sub-social or even eusocial species is discovered in Lower Cambrian strata. Eusociality (Rust and Wappler 2016) is well-known of course in insects such as ants, bees and other hymenopterans; less well-known are the social arachnids such as the spider species *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius* (Theridiidae; Settepani et al. 2013). That the social behavior appears in two different spider families strongly suggests that the behavior developed independently in the two species via convergent evolution. Specialized tasks such as defense and web repair in the eresidid spider colonies are, interestingly, apparently apportioned based on the individual personality of each spider.

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Chapter 12
Parenting Skills

> *Eggs were surely life's first love, and protecting one's eggs was surely life's first urge. Love is that ancient, that pure, that lasting.*
> Sy Montgomery, *The Soul of an Octopus*

Abstract When did nesting behavior and advanced care of young first appear? The microburrow nests of archaeocyathan reef crypt spaces provide the first evidence for: 1, advanced metazoan behavioral complexity, 2, maternal care, 3, nesting behavior, 4, nest site fidelity, 5, evidence for rudimentary eusociality, and 6, evidence for animalian internal fertilization. That such sophisticated behavioral programming appears in the Early Cambrian adds considerably to the perceived magnitude of the Cambrian Explosion.

Graphoglyptid ichnofossils are by far the most interesting type of trace fossil. They are also among the first to be described in the literature. In his 1505 *Paris Manuscript I*, Leonardo da Vinci sketched rows of hexagons next to his sketch of a fossil snail; the hexagons are now interpreted as the earliest published record of the graphoglyptid trace fossil *Paleodictyon* (Baucon 2010; Barras 2012).

The highly geometrical patterns of graphoglyptids such as *Paleodictyon* are striking, and uncertainties regarding their recognition and mode of origin have led to a series of creative inferences, field expeditions, and even submersible voyages to the deep sea floor. Until now, an appreciation of their full nature remained frustratingly out of reach.

This was point was made forcefully by the IMAX video (2003) *Volcanoes of the Deep Sea*. In a climactic scene, Dolf Seilacher finally retrieves from the submersible wide–core sampler an intact sample of sea floor sediment containing an entire burrow network of *Paleodictyon.* This is a moment of high anticipation for Seilacher. Years earlier, during a previous oceanographic expedition, a less–advanced sampling device had scooped up an intact *Paleodictyon* burrow network. Due to a miscommunication on deck, a technician had erroneously washed the sediment sample down a drain before the burrow system could be examined. Seilacher still spoke of this incident with chagrin when he visited Mount Holyoke as Distinguished Five College Lecturer in Geology in the 1980s.

M.A.S. McMenamin, *Dynamic Paleontology*,
Springer Geology, DOI 10.1007/978-3-319-22777-1_12

Finally, with the *Volcanoes of the Deep Sea* cameras running, Seilacher cuts open the sea floor mud to expose the planar polygonal/honeycomb pattern of the trace. The expectation is that we are finally going to learn the identity of the tracemaker. But no tracemaker is in sight. There is a pause, a moment resembling the closing scene in the Humphrey Bogart film noir *The Maltese Falcon*. Seilacher cries out: "Nothing!" The identity of the *Paleodictyon* trace maker remains a mystery.

Miller (2014) lamented that the conundrum threatens to become "some sort of open–ended mystery … [a] stubborn problem … [a] Quest for the Grail." Miller compared the mystery to the resolution to Charles Dickens' last novel *The Mystery of Edwin Drood* (Dickens died before finishing the book), concluding that he would "like to know how the story ends." Seilacher's co–scientist on the expedition, Peter Rona, on first discovering the hexagonal dot pattern during a submersible survey of the sea floor, remarked, not in jest, that it might be the work of miniature space aliens who were colonizing our deep sea floor safely out of sight. In the absence of a metazoan trace maker and decisive evidence to the contrary, this remains both a viable and a scientific hypothesis, although this is unlikely (to say the least) to be the correct explanation for *Paleodictyon*.

As Seilacher (1977) was first to point out, graphoglyptids represent the main type of what is now called an agrichnial trace fossil. In distinction to feeding (fodichnial) or dwelling (domichnial) traces, agrichnial traces are excavated by the trace maker to create a culture chamber for microbes. These farmed microbes later become food for the tracemaker. This is a purely paleobiological inference; to my knowledge agrichnial traces with microbes present have never been recorded in modern aquatic environments. Nevertheless, an analysis of the fractal dimension of motile grazing tracks (fodichnial burrows) and putative agrichnial graphoglyptid burrows (such as *Paleodictyon* and *Spiroraphe*) shows that the fodichnial traces show a consistently higher fractal dimension than do the graphoglyptids, supporting "the hypothesis that graphoglyptids represent agrichnial activity rather than mining or grazing activities" (Lehane and Ekdale 2013). In reply to my December 6, 2015 question posed on *ResearchGate* R^G, paleontologist Joseph Botting replied that the "obvious agrichnial activity on land is of course leaf–cutter ants, and I believe they create distinctive chambers for the purposes of fungus–growing. I'm not aware of any equivalents in marine settings, unfortunately."

The recognition of agrichnial trace fossils in the rock record is thus controversial. However, there is an emerging consensus on what constitutes an agrichnial trace and what does not constitute an agrichnial trace. For example, not all agrichnial trace fossils are graphoglyptids, and vice versa. Graphoglyptids are defined as "geometrically complicated trace fossils preserved on the soles of deep–sea turbidite beds" (Miller 2014). Curiously, considering their potential importance for understanding modern benthic ecosystems, no unequivocal agrichnial burrows have been described from recent aquatic habitats. Of two ichnofossil types that can appear very similar, *Protopaleodictyon* is considered a graphoglyptid whereas *Multina* is not considered a graphoglyptid (Zapata et al. 2016).

Protopaleodictyon is found worldwide throughout most post–Proterozoic deep–water stratigraphic sequences (Crimes and Anderson 1985a, b; Uchman 1998).

These trace fossils typically occur on the soles of distal turbidites, casted by sand by the overlying–turbidite sands, and associated with abundant signs of emplacement current activity such as flute casts, prod marks and groove casts (Vaziri and Fürsich 2007). *Protopaleodictyon* belongs to the *Nereites* ichnofacies, a deep–water ichnofacies known for its geometrically regular burrows (Pemberton et al. 1992; Knaust and Bromley 2012).

Multina is a non–graphoglyptid ichnofossil consisting of networks of meandering traces that can mimic the regular geometric patterns of graphoglyptids. Usually considered a deep–water trace fossil (Kotlarczyk and Uchman 2012), *Multina* can occur in shallower water environments as well (Lima and Netto 2012). *Multina* burrows penetrate several bedding planes, and can develop cross–cutting relationships with flute markings.

Recently discovered specimens of *Multina* from Nevada are evidently feeding traces that nevertheless developed iron oxide–stabilized walls (Zapata et al. 2016). This new report supports previous suggestions that *Multina* may have "been a precursor to the more complex graphoglyptid networks" (Buatois et al. 2009). Although it is true that both *Multina* and *Protopaleodictyon* first appear in Lower Cambrian shallow marine strata (a fact that has implications for the locus and speed of the Cambrian Explosion), it seems likely that the transition from feeding trace to graphoglyptid occurred more than once since the Cambrian Explosion, as both network and spiral graphoglyptids such as *Helmithoraphe* and *Spiroraphe* are known to occur, and these ichnogenera may represent independent acquisition of the agrichnial lifestyle. *Paleodictyon* may indeed be an ichnofossil derived *via* a transition from feeding track to graphoglyptid. There may well be a very ancient association between the two as we saw in the case of *Vaqueroichnus stewarti* n. ichnogen. n. isp. and associated *Helminthoidichnites* isp. *Paleodictyon's* more geometrically–regular pattern and domal–planar upper aspect (upper surface of the network) contrasts with that of presumed feeding traces such as *Multina*. *Paleodictyon's* construction thus reflects the structural/hydrodynamic constraints for optimal function as an agrichnial (microbe–hosting) burrow network.

If we step back for a moment to the Precambrian origin of trace fossils, the distinction between feeding burrow, grazing trace and agrichnial trace fossil is somewhat blurred as we can say that undermat miner traces as seen in the Mina el Mesquite Formation of Sonora, México show aspects of all three types, complete with evidence for Proterozoic farming of the microbial mat. With the biomat able to regrow quickly in many circumstances, undermat burrows may have had an inherently agrichnial aspect. With the appearance of complex geometric graphoglyptid trace fossils, benthic microbial communitites acquired a new type of habitat.

The fact that many types of trace fossils, including the first graphoglyptids, *Multina* and other ichnofossils associated in later times with deep–water sedimentation, adds to the perceived magnitude of the Cambrian Explosion because all of these trace fossil types occur together in the Early Cambrian in shallow water strata. In what amounts to *behavioral telescoping*, a direct counterpart to *phylogenetic telescoping* we discussed earlier, even trace fossils showing complex meander tracks (again, these today are found in the deep sea) occur in the

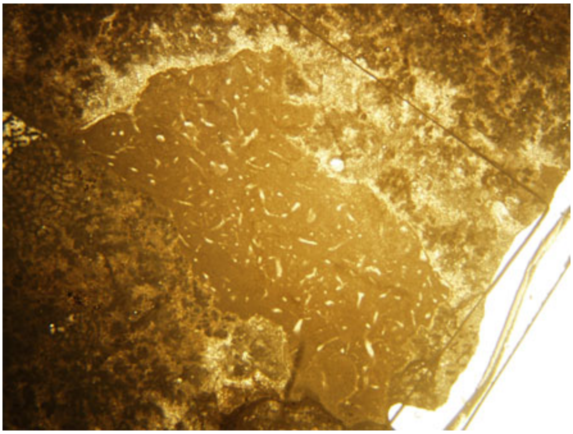


Fig. 12.1 Graphoglyptid trace fossil consisting of microburrow swarms preserved in archaeocyath–algal boundstone. Perimeter burrows occur on the margins of the nest. Perimeter burrows are hypothesized here to have conducted fluids past impermeable barriers adjacent to the crypt next. Branching algae (*Epiphyton* sp.) occur both above and below the crypt nest. Image oriented with stratigraphic up to the top of the photomicrograph. Sample 9 of 3/23/90; IGM 7450b (see also McMenamin (2008), Figs. 2, 5, same slide); Puerto Blanco Formation, base of unit 3, Cerro Rajón, Sonora, México. Width of view 20 mm

short-lived initial Cambrian shallow water ichnofossil assemblage. This singular assemblage deserves to be placed in its own ichnofacies, here named the *Explosion ichnofacies*, where members of the shallow water *Skolithos* ichnofacies, the deep–water *Nereites* ichnofacies, and all intermediate ichnofacies were neighbors in the same environment for a short time. Arguably the most important member of the Explosion ichnofacies, important because of what it tells us about Cambrian animal behavior, is described below (McMenamin 2012).

Enigmatic microburrow complexes reported from Cambrian limestones rich in archaeocyaths from México, Nevada, New Jersey and Mongolia provide evidence for an unusual type of graphoglyptid trace fossil consisting of microburrow swarms (Fig. 12.1). Microburrows in a given swarm were formed by members of the same species, indeed, members of the same cohort. These tiny burrows are preserved as sparry calcite casts in lenticular to irregular patches of lime mud (micrite) several millimeters in greatest dimension (Fig. 12.2). Packed fecal pellets are associated with the microburrow cavity spaces (Fig. 12.3). Pellets in a New Jersey archaeocyath limestone are shown attached to a burrow wall (McMenamin et al. 2000); in Sonoran and Nevadan specimens the pellets are seen inside sheltered cavity spaces.

The void–filling mode of preservation indicates that the burrows were not backfilled, but rather served as conduits for pore fluid circulation. This suggests that these burrow sieve networks represent microbial culture chambers constructed by the tracemakers to cultivate nutritious microbial films within the burrows. As such they represent a three–dimensional variant of the agrichnial, “microbe farmer” niche inferred for graphoglyptids such as *Paleodictyon*.

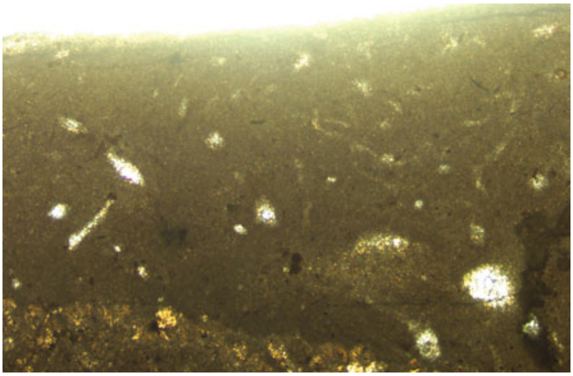


Fig. 12.2 Sparry calcite casts in lenticular patches of lime mud (micrite). Small and larger microburrows are visible. Smaller microburrows are clustered in the center of this nest (*upper right* center on this image). Sample 1 of 12/15/82; Puerto Blanco Formation, unit 3; Cerro Clemente, Sonora, México. Width of view 5 mm

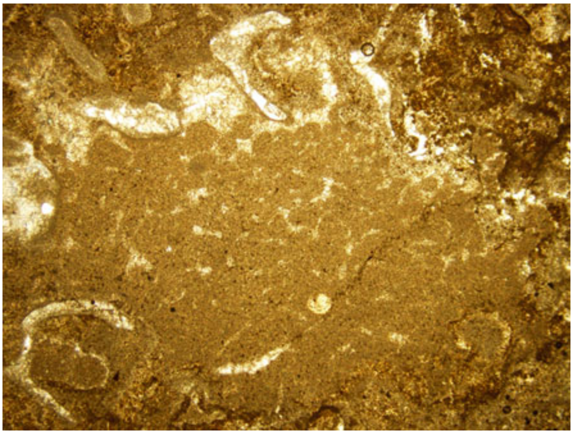


Fig. 12.3 Packed fecal pellets are associated with the microburrow cavity spaces. Pellets are disaggregating to form micrite (lime mud) in the interior spaces of a dead archaeocyath that is being utilized as a microburrow nest crypt space. Pellets are visible in the upper half of the image; microburrows are visible in the lower half of the image where the pellets have undergone disaggregation to form unconsolidated micrite. Archaeocyath–algal boundstone; Sample MM–85–4; Poleta Formation, Barrel Springs, Nevada. Width of view 7 mm; pellet diameters are 200–500 μ

The burrow sieve complexes formed within the interior spaces of archaeocyath skeletons and in crypt spaces within the reef. Considering the co–occurrence of disaggregating pellets and microburrows within these crypt spaces, it appears that the burrowed crypt spaces represent microburrow crypt nests where pellets emplaced by a parent nourished microbial gardens which in turn provided food for the young hatched from eggs laid in the midst of the pellets.

To test the microburrow nest hypothesis, our laboratory applied several methods for obtaining additional information about microburrow swarm geometry. The four most promising methods in this regard were: serial sectioning, 3D rock dissection, CT scan technology and acid etching. Due to insufficient x–ray contrast between the burrows and their micritic matrix, the CT scan (on an X-Tec XT H225L "Metris") proved to be a complete failure in this particular instance. Serial sectioning also proved to be impractical because, even with a thin–bladed saw, too much rock was lost between slices to provide meaningful data about relationships among the microburrows in each swarm.

In a second attempt, we cut a series of thicker slabs (12–17 mm thick) with serially recorded surfaces. Subsequent sectioning of the slabs provided additional data by means of standard thin sections, but we were unable to detect a larger burrow network linking the microburrow nest occurrences, although larger burrows do terminate at the crypt spaces in several examples. Also, the microburrows are best viewed in thin section, and are barely visible on polished slabs of rock due again to insufficient contrast.

Our fourth attempt met with success. A several kilogram sample of archaeocyathan limestone (sample 1 of 12/15/82) was broken into chunks 2–8 cm in greatest dimension and immersed in a weak acetic acid solution. The acid solution was allowed to react with the limestone. After a day, the acid bath was rinsed and the rocks washed in cold water to remove insoluble residue. This sequence was repeated until the rocks had lost approximately half their mass to acid dissolution. At this point, the remaining limestone chunks (with heavily etched surfaces) were rinsed and allowed to dry.

The etched rock chunks were then inspected with a binocular microscope in a search for microburrow nests exposed by acid etching. Fortunately, one of these

Fig. 12.4 Microburrow nests exposed by acid etching. Acid–etched piece of archaeocyathan–algal boundstone, Puerto Blanco Formation, Sonora, México, Sample 1 of 12/15/82. The microburrow nest is the lighter patch of carbonate just below the center of the rock in view (*arrow*). Scale bar in cm

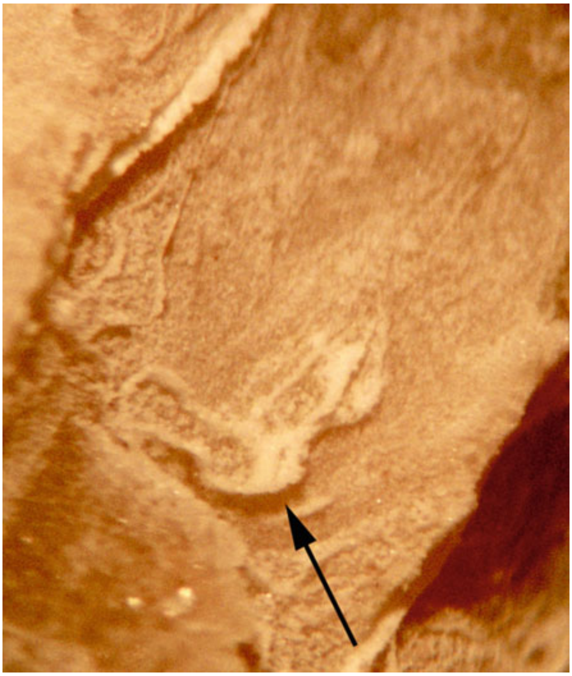


Fig. 12.5 Etched burrow shows a burrow inflection (*arrow*), an obtuse graphoglyptid–type bend in the burrow at approximately a 100° angle. The inclined linear feature above the burrow is a calcite vein. Width of view approximately 1.2 mm

was located on a rock chunk 5.4 cm in greatest dimension (Fig. 12.4). This specimen preserves the outer edge (as viewed from inside the nest) of the crypt sediment, with the walls of the microburrows standing out in relief from the micritic matrix and internal burrow–fill sparry calcite.

This find confirms the inference that the microburrows had stabilized walls—the denser, presumably microbially–influenced walls of the microburrows—were slightly more resistant to acetic acid etching, thus allowing the microburrows to stand out in relief. One etched burrow shows an obtuse graphoglyptid–type bend in the burrow or a burrow inflection (Fig. 12.5). A total of twenty microburrow nests were identified in thin section (nineteen examples) plus a single example on the etched rock surface. Fifteen of the microburrow nests were from México, four from Nevada and one from New Jersey. The irony here is that the two traditional techniques (thin sectioning; acid etching) provided more information about the microburrows than did the serial sectioning and the CT scan.

Regarding the nest hypothesis for these burrows, ichnologist Duncan McIlroy commented (Barras 2012) that the microburrow–nest hypothesis “would be very difficult indeed to prove without finding one with associated eggs.” This is a carelessly worded critique, as it is never possible to “prove” anything in the sciences; it is only possible in science to demonstrate that a particular result is very likely, and even then new information may force revision at any time and without prior notice. The latest science may very well be wrong. Nevertheless, McIlroy was right to ask for additional evidence. I began to search for eggs associated with the microburrows, and I found them.

Three of the most important archaeocyathan limestone deposits in North America occur in: Sonora, México; Nevada; and New Jersey (McMenamin et al. 2000). There are also comparably important limestones in the Yukon Territories–Alaska region, and a suite of rocks of growing importance in Alabama. The latter has just yielded (McMenamin 2015) a specimen of the unusual corolla–bearing spiny archaeocyath *Yukonensis*.

Thin sections of New Jersey archaeocyath limestones yielded the bizarre archaeocyath *Retilamina* (Figs. 3.2, 3.5, 3.6, 3.7 and 3.8). It had not been previously reported from New Jersey (McMenamin and Hussey 2015). As we were finishing the poster for the sessions at the Geological Society of America Annual Meeting in Baltimore, Maryland, on close inspection two of the *Retilamina* slides (there are three in total) showed evidence for microburrowing in cryptic space micrite.

Pellet packing had been observed on previous New Jersey slides (McMenamin et al. 2000), but no microburrows were recognized in that study. On one of the new slides, a circular object 1.8 mm in diameter was ensconced in the burrowed micrite. The circular object was partially filled with smaller, roughly ellipsoidal objects (Figs. 12.6 and 12.7). The best interpretation of this structure is as an egg case or brood chamber with microburrower eggs preserved. The egg structures do not appear to be fecal pellets, because they do not show the partial disaggregation usually shown by pellets, and because they appear to be packed into an enclosed,

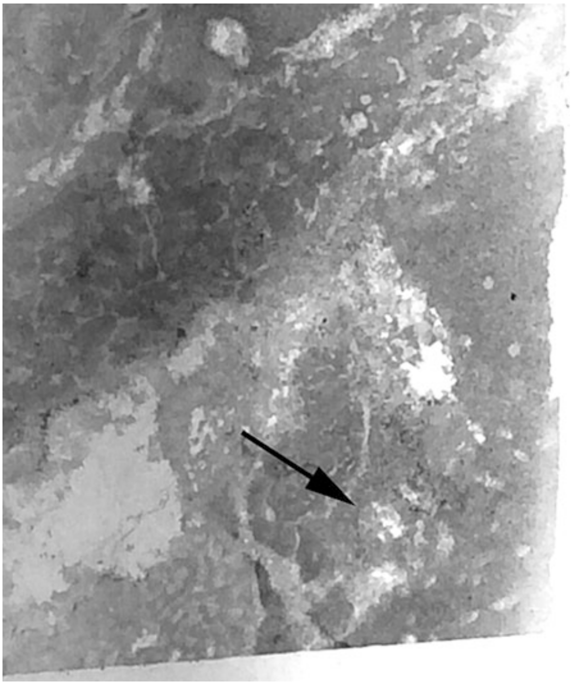


Fig. 12.6 Egg case or brood chamber with microburrower eggs preserved. *Arrow* indicates egg case with eggs. Archaeocyathan carbonate, lower Leithsville Formation, Franklin, New Jersey, field sample 1 of 10/19/89. Width of sectioned rock in view 15 mm

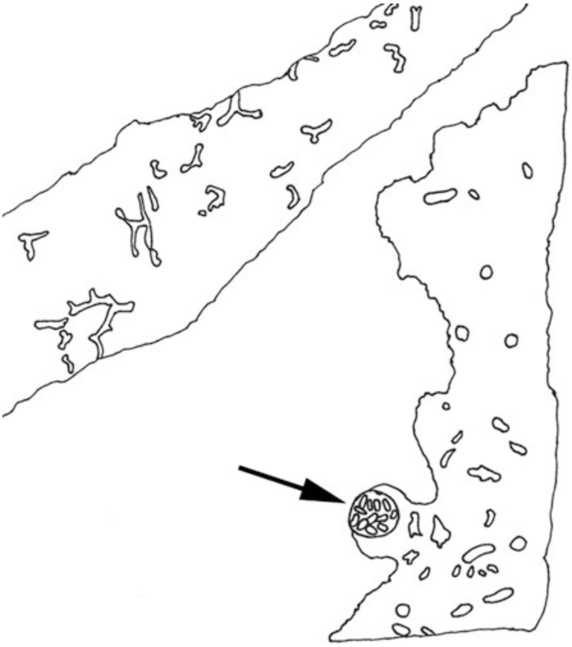


Fig. 12.7 Sketch from previous figure of egg case or brood chamber with microburrower eggs and microburrows preserved nearby. *Arrow* indicates egg case with eggs. A section of *Retilamina* archaeocyath wall is shown at the *upper left*. Width of sectioned rock in view 15 mm

spherical space (egg case) of a type that occurs in other microburrow swarm clusters but never has fecal pellets inside. Also, each egg structure appears to have a smooth rind or eggshell and this feature is never seen in fecal pellets.

The egg case shown in Figs. 12.6 and 12.7 contains twelve eggs (an even dozen!). All twelve are similar in size, roughly 200 μ (long axis) by 100 μ (short axis) forming an elliptical egg. The shape of the eggs and their orientation with respect to one another is reminiscent of the eggs in the egg clusters of the Common Whelk (*Buccinum undatum*). Another alternate interpretation of the structure seen in Figs. 12.6 and 12.7 is that it represents a microoncoid pocket (Dahanayake et al. 1985) known to occur in irregular cavities in stromatolites of the Gunflint Iron Formation of Ontario, Canada. This alternate hypothesis is falsified by the facts that the egg structures are not oriented with their long axes aligned as is the case for the Gunflint pocket microoncoids, and also the structures lack the "irregular external coatings" as seen in the Gunflint microoncoids. Also, the Gunflint microoncoids are much larger, with some reaching over one millimeter in greatest dimension.

Adding to the confidence in the identification of these structures as ancient eggs, one of the best preserved microburrow complexes from Sonora includes a circular structure also interpreted here as an egg case (although without the eggs inside; Fig. 12.8). The egg case structure is not perfectly spherical, but rather is very slightly polygonal in outline, and this same observation applies to the egg case with eggs as seen in Fig. 12.6 from New Jersey. Like its New Jerseyan counterpart, the Sonoran circular structure is also 1.8 mm in diameter. Even if we account for the fact that the plane of section may not be passing through the exact center of these structures

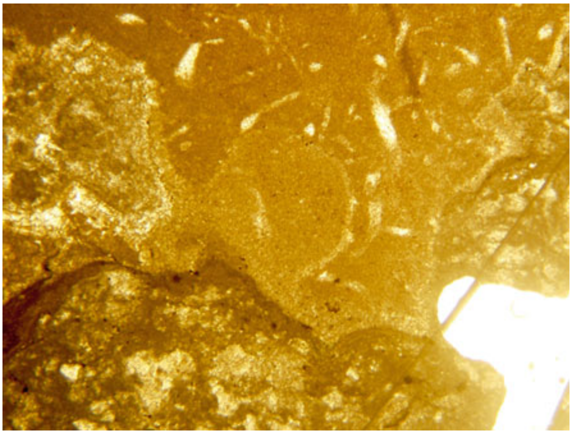


Fig. 12.8 Circular structure interpreted here as an egg case. Sample 9 of 3/23/90; IGM 7450b (see also McMenamin 2008, Figs. 2, 5, same slide); Puerto Blanco Formation, base of unit 3, Cerro Rajón, Sonora, México. Width of view 7 mm

(in which case the 1.8 mm would be an underestimate of diameter), the Mexican and New Jerseyan examples are at least of closely comparable size. We thus now have rather convincing evidence for the nest nature of the microburrow complexes.

It is now possible to formulate a sequence–of–formation scenario for the microburrow nests (McMenamin 2012). Newly formed nests occupied crypt spaces in archaeocyathan reefs and were packed with fecal pellets by one or more parents. One parent, presumably the mother, deposited an egg case adjacent to the pellets. After hatching, the young began to burrow. Pore spaces between the pellets allowed water to circulate through the nest. Microburrows (now calcite–spar filled) developed stabilized burrow walls (Fig. 12.5) to allow pore fluids to continue to circulate as pellets degraded and began to collapse.

The smaller diameter microburrows occur in the center of the nest. The opposite should be the case if the burrow systems were designed for adult occupation, as the larger burrows would have to be centrally placed to ensure adequate pore water circulation. Initial, small central burrows received ample circulation as the outer pellets were still intact at the time. Pellets disaggregated into micrite riddled with microburrows. Some of the latter followed the contours of relict pellets. Nest perimeter burrows conducted fluid past impermeable obstructions.

The null hypothesis, namely, that pellet caches were microburrowed by an unrelated organism, is falsified by the following evidence: microburrowing begins in the center and moves to the peripheral areas; the burrow network has an organized and even geometrical aspect (microburrows have angular bends and in some examples, hexagonal arrays, meaning that they tended to avoid each other); burrow walls are stabilized, remain intact, and evidently do not represent deposit feeding traces made by vagrant burrowers.

Here then is the instruction set for pellet parenting. First, locate and/or excavate a shelter porosity space. Second, pack the space with pellets containing refractory (i.e., hard to digest) organic matter. Third, deposit an egg case within the pellet nest. Fourth, hatchlings feed on microbial gardens while they master locomotion by navigating the temporary porosity space between pellets. Fifth, pellets disaggregate; the apprentice burrowers moving through the micrite renew porosity. A microbial death mask film hardens the inner lining of these "starter" burrows, thus promoting continued "microbial farming."

There are a number of advantages that accrue to this nesting strategy. Hatchlings are protected in their sheltered nest from the onslaught of Early Cambrian predators, and possibly also from waterborne diseases. The strategy provides for a reliable hatchling food source, developed via an agrichnial, ectosymbiotic relationship with microbes lining the nest burrows. Perimeter burrows provide enhanced circulation around impermeable barriers. The cryptic nursery habitat is buffered from any of a variety of environmental insults.

The implications of this scenario are as follows. This is the earliest evidence for "Mom," that is to say, evidence for a parent providing for more than rudimentary maternal (or paternal) care. A tracemaker female was likely responsible for pellet installation, as she was presumably in charge of laying the egg case. Note that male parental involvement cannot be ruled out. This is the earliest evidence for significant parental investment in nest construction.

The advanced behavior reported here occurs in the Early Cambrian, thus adding significantly to the perceived magnitude of the Cambrian Explosion. Furthermore, this burrow type represents the most advanced level of behavioral complexity seen in the entire Explosion ichnofacies, and as such adds greatly to our appreciation of the sophistication of these early burrowers. Note that the Explosion ichnofacies has both an environmental (shallow water) and temporal (Early Cambrian) connotation.

As Dolf Seilacher discerned in the 1950s, the signal characteristic of sedimentation across the Proterozoic–Cambrian boundary is the transition from microbial matgrounds to bioturbated substrates (Seilacher 1956). This research was really our first hint of an Explosion ichnofacies, although in the 1950s very few realized how unique this ichnofacies actually was. The transformation from matground to burrowed sediment has profound implications for marine sedimentology and geochemistry. A most interesting aspect of the change is the ephemeral appearance of unique types of sedimentary rocks, such as flat pebble conglomerate (or FPC; Sepkoski 1982). FPCs represent the final gasp of the widespread biomat–influenced sedimentation that dominated the marine realm for most of Precambrian time. FPCs appear in the late Proterozoic and became rare after the Ordovician.

The microburrow complexes described here may represent another unique sedimentation type that vanished later in the Paleozoic. The microburrows are of similar morphology but of mixed diameters within a single swarm, indicating that a community consisting of a conspecific cohort consisting of hatchling metazoans and their microbial ectosymbionts formed the burrow sieve complex. The nursery aspect of these microburrow sieve complexes provides the earliest evidence for rudimentary eusociality in the fossil record, and also provides the first indirect evidence for animalian internal fertilization, if we assume that a gravid female laid the eggs.

The recognition of microburrow nests has profound implications for our interpretation of the Cambrian transition event. These nests represent the earliest fossil evidence for nesting behavior. Such sophisticated behavioral programming is

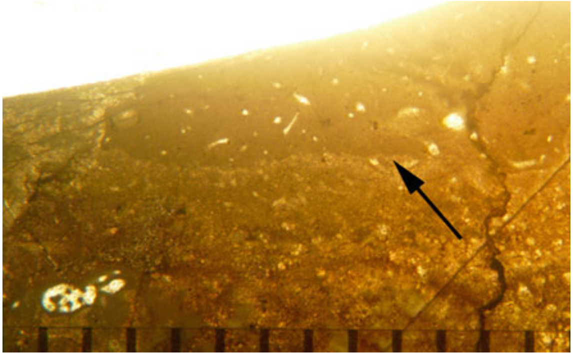
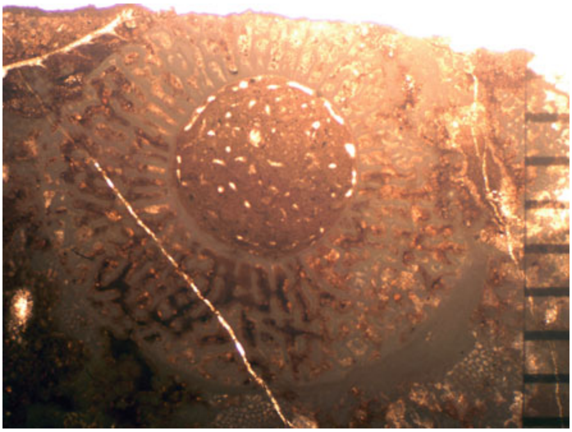


Fig. 12.9 Microburrow nest cavity with evidence for nest reoccupation. *Arrow* indicates horizon between successive microburrow nest occupations of the cavity space. The base of the first nest is visible as a diffuse oxidized zone just above the small archaeocyath skeleton at the *lower left* of the image. Note empty egg case at the far *left* end of the second microburrow nest. Faint microburrows remain visible in the earlier microburrow nest. Sample 1 of 12/15/82; Puerto Blanco Formation, unit 3, Cerro Clemente, Sonora, México. Scale in mm

remarkable for animals living close to the Proterozoic–Cambrian boundary. This discovery contributes substantially to the perceived magnitude of the Cambrian Explosion. Figure 12.9 shows just how sophisticated this behavior was, as we see here a microburrow nest cavity space that was reoccupied by a second phase of nesting, similar to the nesting behavior of modern birds, many of whom reoccupy the same nest season after season. This may imply a degree of "cave" nest–site fidelity comparable to cavity reoccupation among Blue–Footed Parrots (*Amazona aestiva*) in the Chaco of Argentina (Berkunsky and Reboreda 2008).

Finally, consider the interesting microburrow nest shown in Fig. 12.10, where the nest is formed within the central cavity of a dead archaeocyath. Note the perimeter (ventilation) burrows running along the carcass of the archaeocyath inner wall.

Fig. 12.10 Microburrow nest cavity in central cavity of archaeocyath. Cerro Clemente, Sonora, México, Puerto Blanco Formation, field Sample 1a of 12/15/82. Scale in mm



The biostratigraphically important treptichnid trace fossil *Treptichnus pedum*, one of the earliest complex trace fossils, is conventionally used as an index ichnofossil to define the base of the Cambrian in Proterozoic–Cambrian stratigraphic sequences, although some studies suggest that its stratigraphic range does in fact extend downward into the latest Proterozoic. Many treptichnid trace fossils show a vertical component to each lobe of the burrow, thus in addition to the presumed deposit–feeding behavior of the tracemaker, some and perhaps many treptichnid burrows may also have performed an agrichnial function. The two feeding modes are not necessarily mutually exclusive, even within a single burrow system.

Of particular interest in this regard is the ichnofossil *Treptichnus coronatum* from Member 2 of the Chapel Island Formation, Grand Bank Head, Newfoundland (Crimes and Anderson 1985a, b). The coronet shape of the trace fossil implies agrichnical feeding in preference to deposit feeding. As *T. coronatum* bears a notable resemblance to *T. pedum*, it seems likely that, in terms of the evolution of complex burrow types near the basal Cambrian boundary, that advanced agrichnial trace fossil types (*Protopaleodictyon*, *Paleodictyon*, *Squamodictyon*, *Treptichnus coronatum, Treptichnus pedum*) actually preceded the development of complex deposit feeding trace fossil types (Fedonkin 1978) such as the "bundled tube" spreite–bearing trace fossils currently placed in the ichnogenus *Phycodes*. Finally, if we reinterpret *Archaeotrypa secunda* from the Poleta Formation, Nevada as an ichnofossil preserved by sparry calcite filling the burrow network (Kobluk 1983), then *Archaeotrypa secunda* joins the agrichnial plexus based on its close geometrical resemblance to *Paleodictyon*. This inference has important implications, namely, that as counterpart to the flat pebble conglomerates (FPCs) that precede the highest ichnofabric indices (i.e., heavily burrowed sediments), basal Paleozoic complex agrichnial trace fossil types may have developed just prior to morphologically–complex deposit feeding tracks. The microbial lining to newly formed microburrows became an important new food source, a way to indirectly digest the refractory organic matter in the pellet–derived micrite that was also able to serve as the food resource for a cavity brood chamber. The nearly simultaneous appearance of both agrichnial and treptichnid trace fossil types near the Cambrian boundary provides eloquent testimony to the dramatic increase in the sophistication of animal behavior at this time.

We can now at last effectively address the graphoglyptid controversy. In a remarkable 2009 paper in *Deep Sea Research II*, Dolf Seilacher and Peter Rona presented conflicting interpretations of *Paleodictyon* in the same paper (Rona et al. 2009). Seilacher argued that these graphoglyptids are ectosymbiotic microbial culture chambers, hence they represent Cambrian to Recent trace fossils. Rona argued that graphoglyptids are body fossils of some unknown organism, such as a sponge, a xenophyophore protist, or even an Ediacaran.

Recall that the main conundrum regarding graphoglyptids is that no actual trace maker, no cytoplasm, no sponge spicules, no excess microbial biomass, nor the actual remains of the presumed hexagon network organism, has ever been recovered in modern graphoglyptid examples. The solution to the puzzle is as follows.

Modern graphoglyptids are empty nests. The young have long since departed, leaving behind an empty nest that lasts decades or more on the deep sea floor.

Modern graphoglyptids "may last for tens to hundreds of years under the prevailing conditions" at the TAG hydrothermal field at the mid–Atlantic Ridge. Refractory organics are depleted by the time the nests are collected by researchers (hence only background levels of bacteria are detected). Recall that Seilacher, speaking in Stephen Low's IMAX video *Volcanoes of the Deep Sea*, exclaims, in his failed search for the trace maker animal, "Nothing!" The reason for this is that the microbial garden has been harvested.

In conclusion, graphoglyptids are trace fossils, ectosymbiotic mushroom farm nests (or, better to say, microbial farm honeycomb networks?) constructed for the care and feeding of hatchlings. They first appear in the Early Cambrian in both carbonate (microburrow nests) and silica mud/siliciclastic environments (*Protopaleodictyon*). Nest perimeter microburrows provide enhanced circulation for nests in cavity spaces. Geometrical network traces such as *Paleodictyon* and *Protopaleodictyon* have inherently better circulation due to their more planar (and hence higher surface area) aspect. Graphoglyptid nesting behavior migrated into deep water during the Phanerozoic to avoid increasingly dangerous shallow water habitats. The nests are living fossils, optimized for passive seawater flow through the burrow nest network.

It remains a project of compelling scientific interest to capture a live *Paleodictyon* tracemaker, and/or to find a nest that is still sheltering the fry. There is a good chance that this animal has a "living fossil" aspect that could be vital for advancing our understanding of the Cambrian Explosion. The creature is probably some sort of small arthropod or arthropod–like form, considering that arthropod brood–rearing behavior within the carapace has been reported from both the Early Cambrian (egg brood in the bivalved arthropod *Kunmingella douvillei*; Chengjiang biota) and Middle Cambrian (eggs and embryos in *Waptia fieldensis*; Burgess Shale; Caron and Vannier 2015).

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Chapter 13
First Fruits

> *Time has endless rarities, and shows of all varieties; which reveals old things in heaven, makes new discoveries in earth, and even earth itself a discovery.*
>
> Thomas Browne (1605–1682), *Hydriotaphia*

Abstract When did the first fruits appear? The 'fruit grade' of plant evolution was apparently attained by multiple lineages (Caytoniales, angiosperm ancestors) simultaneously in the earliest Jurassic at a time of profound global cooling in the wake of a major mass extinction. Where fossils are rare, due to their enclosing strata being deposited shortly after a mass extinction or for other reasons, each fossil discovery is potentially critical.

The *Dynamic Paleontology* methodology advocated here may be applied to field research in exotic locales, but can be equally successful when applied to sites close at hand such as one's own backyard. Figures 13.1 and 13.2 show a paving stone in my back yard in South Hadley, Massachusetts, with a fossil of a Jurassic cycad cone. The stone was in place when we bought the house in 1993. I realized early on that the stone had some sort of interesting fossil, but for years I could not make out exactly what sort of organism it represented.

The mystery was solved when, on a field trip in my Paleontology and Stratigraphy course at Mount Holyoke College, student Zoe Brown found an intriguing (Figs. 13.3 and 13.4) riverside float specimen at the Beachgrounds fossil site in South Hadley Falls, Massachusetts. At first, I thought that the specimen represented a variation on Mesozoic lacustrine mat pustules, for as we have seen these are common in the Connecticut Valley Mesozoic lake strata. On closer inspection, however, the mat pustule hypothesis did fit the features we were observing in the specimen. The bumps occur in too regular a configuration, and when seen with proper lighting, they resolve into a cone structure supported by a stalk. This specimen, as does the specimen in my paving stone, represents the fossil of the cone of a Jurassic cycad. These are the first two such specimens reported from Connecticut Valley Mesozoic lacustrine strata, and thus represent important paleobotanical discoveries.

M.A.S. McMenamin, *Dynamic Paleontology*,
Springer Geology, DOI 10.1007/978-3-319-22777-1_13

Fig. 13.1 Fossil Cycad Cone Species 1. Male cone, cf. *Cycas circinalis*, the Queen Sago. Lower Jurassic, Portland Formation, paving stone in residential stone path, South Hadley, Massachusetts. Scale bar = 2 cm

Fig. 13.2 Fossil Cycad Cone Species 1. Interpretive sketch of previous illustration. The cycad cone split in half just before burial; *dashed lines* show broken edges of the cone where its interior is exposed. Scale bar = 2 cm

We were previously aware that cycad fossils occurred in the nearby town of Granby. On the same street where I live, just across the Granby line, an old quarry yielded an important plant fossil for Mount Holyoke paleontology. Recovered by enthusiastic students, the find represented the first discovery of the cycadeoid plant *Ptilophyllum* in the Connecticut Valley. Our report of the find (McMenamin and Ulm 2004) was the cover story for *Northeastern Geology and Environmental Science*.

Fig. 13.3 Fossil Cycad Cone Species 2. Male cone, cf. *Cycas circinalis*, the Queen Sago. Lower Jurassic, Portland Formation, field sample 1 of 3/10/2015; river shoreline near Beach Grounds Park, South Hadley Falls, South Hadley, Massachusetts, Lat 42.212499 N, Long 72.593193 W. Lacustrine shale, Portland Formation, South Hadley Falls, Massachusetts; Late Hettangian Stage (Lower Jurassic), *Corollina meyeriania* palynofloral zone, 201.2 million years age. Scale bar = 2 cm

Triassic–Jurassic cycads and cycad–like fossils are known from the Pangean rift basins of the Eastern United States seaboard, but they are rather uncommon and represented by only a relative handful of localities stretching from the Richmond Basin, Virginia to the Connecticut Valley (Table 13.1).

Not counting the new cycad cones, only six genera of cycads have been reported from the extensive (and heavily prospected and collected, by generations of geology classes) rift basin strata. The reason for this, as alluded to in a previous chapter, is that Earth had just gone through a harrowing double–phased mass extinction (Permo–Triassic and End Triassic), the worst double blow the world had ever experienced, at least since the Cambrian Explosion. In the Early Jurassic, the world was still in the recovery phase, and cycads (alive today but threatened by overharvesting by horticulturists and hobbyists) were part of the recovery biota. Their fossil record as shown above suggests that their populations were scattered. Other plant fossils such as the early conifer cheirolepidaceans (a juniper–like form) are much more common in the Connecticut Valley and indicate that woodlands had begun to recover by the Early Jurassic.

Cycads appear to be holdovers from the Mesozoic, but the concept that they represent living fossils has been challenged with indications that living genera underwent species diversification a mere 12 million years ago (Rull 2012). Nevertheless, cycads have been extant since the Permian and still have a remarkably extensive geographic distribution in the tropics, stretching from western México to Sri Lanka (*Cycas circinalis*) to the east coast of Australia and the

Fig. 13.4 Fossil Cycad Cone Species 2. Interpretive sketch of previous illustration. The cycad cone is attached to a vertical stalk. Approximately 51 cone leaflets are still attached to the cone; many of them taper upward to a point. Tiny rectangular chips of coal are embedded in the surface of many of the seeds. Scale bar = 2 cm

Table 13.1 Cycadeoid fossils of the Eastern United States Mesozoic Rift Basins

Taxon	Locality	Age
Cycadinocarpus chapini	Durham, Connecticut	Triassic–Jurassic
Dioönites longifolius	Newark Series, New Jersey	Triassic
Macrotaeniopteris magnifolia	Richmond Basin, Virginia	Upper Triassic
Otozamites brevifolius	Durham, Connecticut	Triassic–Jurassic
Otozamites latior	Durham, Connecticut	Triassic–Jurassic
Otozamites sp.	Durham, Connecticut	Lower Jurassic
Ptilophyllum sp.	Hartford Basin, Massachusetts	Lower Jurassic
Zamites powelli	Richmond Basin, Virginia	Upper Triassic
cycad cone 1	Hartford Basin, Massachusetts	Lower Jurassic
cycad cone 2	Hartford Basin, Massachusetts	Lower Jurassic

southern tip of the Japanese archipelago. The cycad cones shown in Figs. 13.1, 13.2, 13.3 and 13.4 show close resemblances to those of living genera and species (Varghese et al. 2010) such as *Cycas circinalis* and *Encephalartos*. Several observers have remarked that it is remarkable that cycads still exist, considering that their characteristically slow cambial growth puts them at a competitive disadvantage when compared to the comparatively rapid growth of angiosperms. Their foliage and seeds are festooned with a toxic mix of poisonous and/or carcinogenic compounds, and this no doubt discourages many grazers from feeding on cycads.

The angiosperm lineage, the flowering plants, is descended from gymnosperm ancestors of the Early Mesozoic. As is the case for cycads generally, the fossil record of the earliest angiosperm ancestors is poor, and any new information about angiosperm origins is of potentially great scientific interest. Angiosperms underwent a tremendous genus and species diversification during the Early Cretaceous; the timing of this flowering plant radiation has led several authors to speculate ("Did dinosaurs invent flowers?") that dinosaurs facilitated the spread of flowering plants though habitat disturbance and other factors (Barrett and Willis 2001).

The aftermath of both the end Permian and end Triassic mass extinctions likely contributed to the situation where both cycads and potential angiosperm ancestors are rare as fossils in the rift basin strata of the Eastern United States. However, as noted above, such fossils may be found with patient searching and a dedicated research program, particularly one that utilizes sharp–eyed geology students to help find the scattered fossils.

The geology of the Mesozoic Connecticut Rift Valley played a critical, early role in the development of historical Earth sciences in the United States. In spite of two centuries of research (Cleveland 1816), fossil plants of these Triassic–Jurassic strata are still poorly known due to a paucity of well–preserved material. Most fossils are fragmentary carbonized impressions. Stem fragments of cheirolepidaceous conifers (represented by leafy material assigned to *Pagiophyllum* and *Brachyphyllum*) are relatively common among the identifiable pieces in shales of the Portland Formation, the lacustrine rock unit spanning the Triassic–Jurassic boundary that has yielded abundant mat pustule specimens as described earlier. The low plant diversity in this formation has been attributed to the fact that the earliest Jurassic flora is part of a recovery biota that survived the aftermath of the Triassic–Jurassic extinction, the severity of which has been compared to the extinction at the end of the Cretaceous Period (Olsen et al. 2003).

During a Mount Holyoke field trip, geology student Taylor Bennett collected a carbonized seed fern (pteridosperm) ovule (Fig. 13.5) from float on the east bank of the Connecticut River near Beachgrounds Park in South Hadley Falls. This was the same locality that subsequently produced the second species of cycad cone fossil (Figs. 13.3–13.4). The Beachgrounds locality remains a productive site because each year, spring flooding along the Connecticut River exposes new fossiliferous shale, continuously renewing the site.

Returning the specimen to the Mount Holyoke Paleontology laboratory, analysis showed that the fossil was a Caytoniales seed fern cupule. The fossil occurs in strata belonging to the South Hadley Falls member of the Portland Formation, as indicated by an asterisk in the partial stratigraphic column shown in Fig. 13.6.

Figures 13.5 and 13.7 show a gigantic (1 cm in greatest dimension) caytonialid seed fern cupule from a Mesozoic seed fern (*Caytonia* sp.). Seeds are absent from

Fig. 13.5 *Caytonia* sp. Pteridosperm (seed fern) cupule preserved in lacustrine shale, Lower Jurassic Portland Formation, South Hadley Falls, Massachusetts. Fossil preserved as carbonized impression and internal mold of cupule interior. Field sample 1 of 4/3/2014; IGSN: MHC008954, river shoreline near Beach Grounds Park, South Hadley Falls, South Hadley, Massachusetts, Lat 42.212499 N, Long 72.593193 W. Lacustrine shale, Portland Formation, South Hadley Falls, Massachusetts; Late Hettangian Stage (Lower Jurassic), *Corollina meyeriania* palynofloral zone, 201.2 million years age. Scale in mm

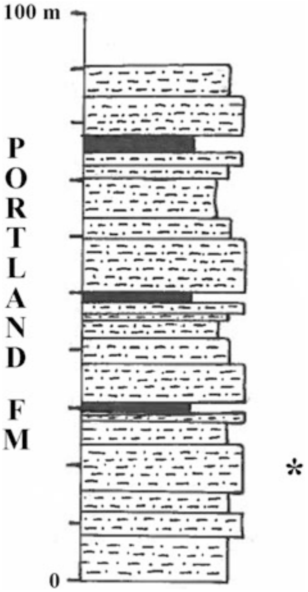

Fig. 13.6 Stratigraphic column showing the stratigraphic section on the South Hadley side below the Holyoke dam, Stop 3 of Olsen et al. (2003). Asterisk (*) shows approximate stratigraphic position of *Caytonia* sp. reported here. Thickness scale in meters. Geological symbols key: black, dark lacustrine shale; dash and dot pattern, mixed lacustrine siltstone and shale. Portland Formation, South Hadley Falls, Massachusetts; Late Hettangian Stage (Lower Jurassic), *Corollina meyeriania* palynofloral zone, 201.2 million years age

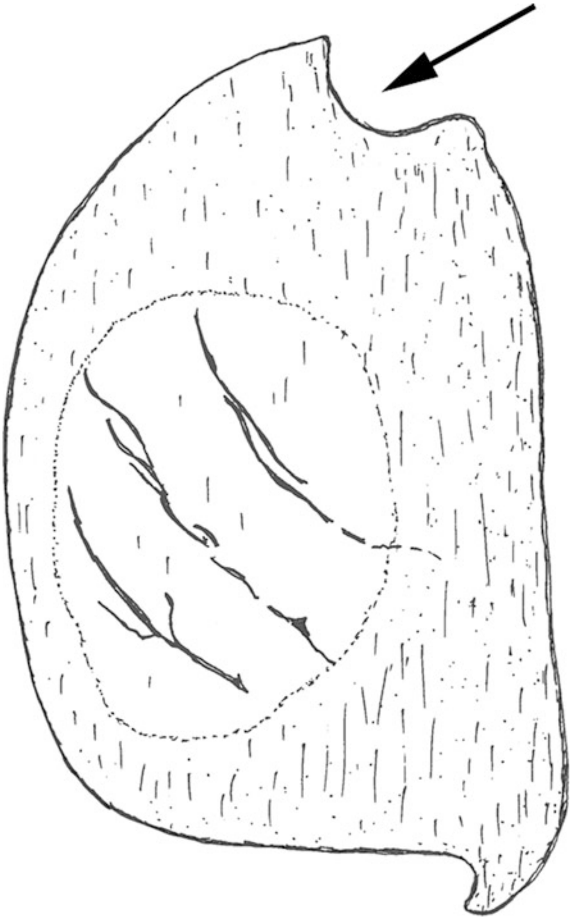

Fig. 13.7 *Caytonia* sp. Sketch of pteridosperm cupule preserved in lacustrine shale, Lower Jurassic Portland Formation, South Hadley Falls, Massachusetts. Arrow indicates arcuate scar where the cupule attached to the ovule–bearing axis. Field sample 1 of 4/3/2014; IGSN: MHC008954

the cupule and may have been dispersed prior to preservation by carbonization. Tiny pyrite crystals are visible on the surface of the fossil seed fern cupule.

The fossil is a berry–like, multiovulate cupule bearing an inner integument consisting of widely spaced, anastomosing fibers ("longitudinally directed fibers" of Taylor et al. 2009; Taylor and Taylor 2009) and finely striate epidermis. The cupule shows an arcuate scar (Fig. 13.7, arrow) where it attached to the (presumably megasporophyll) ovule–bearing axis. A blunt tip, resembling the distal tip of a snow pea pod (*Pisum sativum* var. *saccharatum*) occurs at the distal end of the cupule. The cupule is very roughly rectangular, with relatively straight inner and lower edges that meet to form a blunt, snow pea–like distal tip that curves toward the lower edge.

Caytonia is a "form genus" for reproductive plant structures found in association with the fossil foliage genus *Sagenopteris* and the pollen–releasing organ (microsporophyll) *Caytonanthus*. Unhelpfully, these three parts of plants are rarely found united all together, hence the need for the form genera (Harris 1933, 1940, 1951). Close association of *Sagenopteris* and *Caytonanthus* in Early Jurassic floras of Hope Bay and Botany Bay, Antarctica is in accord with the assignment of both form genera fossil types to the Caytoniales (Reese 1993). *Caytonia* serves as form genus for the ovule structure of the Caytoniales, a seed fern order established by Hamshaw Thomas (1925). The phylogenetic relationship between the Caytoniales and angiosperms is a contentious topic of enduring paleobotanical interest (Krassilov 1977, 1984). There are reasons to believe that there is an ancestor–descendant relationship between the Caytoniales and the angiosperms (Barbacka and Bóka 2000). Even if this is not the case, both groups were approaching the same evolutionary grade. Doyle linked *Caytonia* to angiosperms on account of shared features such as net venation, loss of nucellar vasculature, anatropous cupules, bitegmic ovules and unraised guard cell poles. A strict consensus of 18 most parsimonious trees places *Caytonia* as the genus closest to the angiosperms (Doyle 2006).

The degree to which the features listed above represent homoplasies (shared features developed by convergent evolution) and which represent homologies (features of shared descent) is uncertain, however, leading Doyle (2006) to remark that new "data on currently unknown characters of glossopterids, 'Mesozoic seed ferns,' and Bennettitales are needed to test these [phylogenetic] hypotheses." Wang (2010) argued that the cupule–bearing organ in the Caytoniales is a branch rather than a pinnate megasporophyll, because the female reproductive organs of the caytonialid *Paracaytonia hongtaoi* show spiral arrangement of cupules along the reproductive axis. This is a pattern one might expect for cupules derived from branches. Clearly, any additional data bearing on the morphology of the Caytoniales will be a welcome addition to efforts to the elucidate the origin of angiosperms.

Although seed ferns may not in fact be directly ancestral to angiosperms (Zavada and Crepet 1986), it now seems clear that the Caytoniales first attained the "fruit grade" of propagule evolution in vascular plants. Andrews (1961), who seriously considered a caytonialid ancestry for the angiosperms, notes that the Caytoniales "were very close to the angiospermous state and suggest one way in which the carpel may have evolved." As such, the genus *Caytonia* is among the earliest plant genera in which the seeds are almost completely enclosed. The very fleshy cupule of the Bulgarian caytonialid *Reymanownaea kvacekii* Barbacka and Bóka is filled with an amorphous substance that is lipid rich, possibly representing the remains of nutritious fruit flesh.

The large size and abundant pyrite crystals (which typically occur where there was abundant organic matter) associated with the Massachusetts *Caytonia* sp. suggest that this reproductive structure was relatively rich in organic matter and probably somewhat fleshy. An inner cuticle has been identified in *Caytonia sewardii*, leading Harris (1951) to infer the possibility that the cupule bore a berry–like, fleshy integument. *Caytonia* sp. and *Reymanownaea kvacekii* indicate that plants attaining what might be called the fruit grade of development were part of the land biota by the Early Jurassic. In any case, a level of organization approaching angiospermy (i.e., near total ovule enclosure) was achieved by advanced seed ferns by the Cretaceous (Stockey and Rothwell 2008).

The outer edge of the Massachusetts cupule forms a relatively smooth, convex curve that terminates at the arcuate detachment scar, in accordance with the inference of Andrews (1961) that the cupules were "dropped by a dehiscence mechanism." The cupule at 1 cm is larger than the 7–8 mm wide, fleshy seed–rich reniform cupule of *Reymanownaea kvacekii*. Although large for the Caytoniales, *Caytonia* sp. described here is dwarfed by Paleozoic medullosalean ovules such as that of *Pachytesta incrassata* where the structures are over 10 cm long and 5 cm wide. These structures may be homologous with cupules (Christopher Cleal, written communication, 2014).

The presumption here is that multiple seeds were dispersed from the *Caytonia* sp. cupules after the structure reached maturity, but the number of seeds per cupule is unknown. The inner integumental longitundinal fibers (the three diagonal black bands with anastomosed fibers visible in Figs. 13.5 and 13.7) are very similar to those of *C. sewardii*, however, they are more widely spaced than in *C. sewardii* and in the Massachusetts *Caytonia* they are positioned at an approximately 50° angle to the relatively straight inner edge of the cupule. The anastomosing nature of the inner integument longitudinal fibers is in accord with the net venation of the *Sagenopteris* assumed to be the foliage of Caytoniales, and indeed a net–like pattern is sometimes visible on the surface of the cupule of *C. sewardii*. Whether or not the snow pea–like distal tip of the cupule in *Caytonia* sp. is a stigmatic lip is unknown.

The *Caytonia* specimen is assigned here more precisely to the Late Hettangian Stage (Lower Jurassic), *Corollina meyeriania* palynofloral zone, and is thus 201.2 million years old. The transition from the underlying Park River member to the overlying South Hadley Falls member of the Portland Formation is marked by a transition from fossil plants dominated by small–leaved conifers (papillate stomata, thick cuticle) to conifers with larger leaves (Olsen et al. 2003). Based on McLaughlin cycles and Milankovich cyclostratigraphy, the South Hadley Falls section near the Holyoke Dam is 1.2 million years younger than the 200 million year Triassic–Jurassic mass extinction, in other words, the rocks are approximately 201.2 million years old. The strata at South Hadley Falls appear to have been deposited just after the beginning of the Jurassic Period, and just after the mass extinction.

Although fossil pollen perhaps attributable to seed ferns ("possible pteridosperm pollen" of Olsen and coauthors) has been found in Connecticut Valley strata, until now no pteridosperm foliage or reproductive organs have been reported from the Hartford or Deerfield Triassic–Jurassic rift basin strata in Massachusetts and Connecticut. The occurrence of *Caytonia* sp. in the South Hadley Falls member of the Portland Formation provides unambiguous evidence for the presence of seed ferns in the Hartford Basin.

Olsen et al. (2003) infer that the strata at the South Hadley Falls/Holyoke Dam site were deposited at a time of "apparent recovery" from super–greenhouse conditions. The implication of course is that runaway global warming caused the end Triassic extinction. The change in leaf size noted above, from small coniferous foliage in the Park River member of the Portland Formation to large coniferous leaves in the South Hadley Falls member, accords well with inferences that leaf size is inversely correlated to ambient temperature (Guerin and Lowe 2012; Guerin et al. 2012; but see Duncan 2012). Fruit size has also been inversely correlated to temperature (Bassanagari and Kala 2013), but this is typically linked to fruiting plants that require a winter chill for normal fruit development. As the data set is still small with regard to the paleobotanical record in the Hartford Basin, it may be premature to infer an inverse correlation between leaf and/or reproductive organ size and climate. Nevertheless, the large size of our specimen of *Caytonia* sp. may be plausibly linked to global cooling experienced in the wake of super–greenhouse conditions at the end of the Triassic.

If this is the case, namely, that fruiting bodies were the result of a phase of global cooling after extreme hothouse conditions, then the development of fruits and seeds on which our agricultural systems depend owes much to the recovery after the End Triassic mass extinction. A topic well worthy of consideration is whether or not there is an analogy between the Snowball Earth glaciation crisis (immediately followed by the emergence of Ediacarans and animals), and the Permo–Triassic and End Triassic extinction crisis (immediately followed by the emergence of fruited seeds). Could this represent an important corollary of environmental convergence? If so, it may truly be said that great crises provide the biosphere with great opportunities.

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Chapter 14
Pandora's Pithos

Be bold and mighty forces will come to your aid.
Johann Wolfgang von Goethe (1749–1832)

Abstract What caused the Cambrian Explosion? The geologically simultaneous appearance of numerous animal phyla at the base of the Cambrian was caused by an epidemic of Cambrian Explosion (CE) virus, a "phylagen" (as opposed to pathogen) that was able to infect and reconfigure metazoan morphogenetic fields and genomic kernels. The morphological change in each infected animal lineage was comparable to what happens during the metamorphosis from caterpillar to butterfly. The CE virus was able to reach marine pandemic proportions due to both environmental disruption and habitat destruction during the transition from biomat world to the Paleozoic. A nidus animal released CE virions that infected embryos of other species, thus generating the new phyla.

The preceding chapters of this book provide examples of how one might conduct research by means of the methods of *Dynamic Paleontology*. I have waited until this point in the book to give a precise explanation of *Dynamic Paleontology* methodology. Its origins may be traced back to the disciplined research program initiated by the great anatomist and paleontologist Georges Cuvier (Rudwick 1997). With regard to the past behaviors and ecologies of extinct organisms, Cuvier wrote the following in 1798:

> One could even, with a little more boldness, guess [*deviner*] some of its habits; for the habits of any kind of animal depend on its organization, and if one knows the former one can deduce [*conclure*] the latter. After all, these conjectures would hardly be any more hazardous than those that geologists will find themselves obliged to make …

This type of conjectural approach, involving as it does the generation and testing of multiple hypotheses, has been criticized by scientists of Russia and the East in their critique of western science. Vladimir Vernadsky wrote in 1926 that such approaches "hinder scientific research by limiting its final results; by introducing conjectural constructs based on guesswork (*ugadyvat'/ugadat'*), they obscure scientific understanding." Although Vernadsky's cautionary comments are certainly

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worth pondering, it seems clear to me at least that if we are to learn more about the history and development of life, particularly during the critical Cambrian Explosion interval, we must proceed with a Cuvierian approach to the scientific analysis of events of the remote past.

Following then are the main elements of the *Dynamic Paleontology* approach, a methodology that may be applied to all the sciences. Its application will keep the conduct of science fresh, alive and directed towards the search for truth. It will avoid the self–delusional trap of group–think, an emerging danger in some scientific circles.

Here are the *Twelve Rules of Dynamic Paleontology*:

1. Chose paleontological problems wisely, but always incline toward solving the biggest or most difficult problems.
2. Be grateful that laws of nature actually exist. Finding them is the ultimate goal of paleontological research.
3. Acquire the proper search image if you are seeking particular fossils in the field.
4. Seek morphological confirmation of any inferences you may wish to make about baüplan geometries. But go ahead—do not be shy about making such inferences.
5. An initial examination of the strangest cases is the best way to study overall system dynamics. Sometimes the apparent 'afterthought'—such as for example the 'add on' chapter at the end of a science text—has the most important information.
6. Rigorously test mathematical models and computer simulations with common sense.
7. Beware of false signals, particularly of the statistical variety.
8. Beware the pitfalls of making paleoecological inferences based on limited data, but be bold when authentic patterns begin to emerge.
9. Be ready to synthesize key observations. Recall that paleontology necessarily involves a choppy and incomplete dataset; use this to your advantage. Proper use of the evidence at hand, from any source, requires the paleontologist to engage in lateral thinking. This is actually *a great advantage*. The incompleteness of the fossil record is a strength, not a weakness, because it forces us to 'think outside of the box'.
10. Multiple independent investigations coming to identical conclusions are the best way to verify scientific facts.
11. Seek the solutions to paleontological problems that generate predictions that are likely to be confirmed by subsequent research. Example: one prediction presented in this book is that something approaching eusociality will eventually be shown to occur in the Lower Cambrian fossil record.

Even apparently unlikely predictions can bear fruit if carefully crafted. In *Hypersea: Life on Land*, Dianna and I made (McMenamin and Schulte McMenamin 1994) the following prediction:

> *4. Photoautotrophic land animals (none of which are known today or in the fossil record) that contain either eukaryote symbionts or chloroplasts in their tissues will be found to have lived at some time during the past 500 million years—they may even still be alive.* We frankly admit that the absence of photosynthetic land animals presents a stumbling block for the Hypersea hypothesis. This is because land animal tissues would seem to present an inviting hypermarine environment for photosynthesizing microbes. [Italics in original.]

Kerney et al. (2011) reported the discovery of photosymbiotic microbes (the alga *Oophila amblystomatis*) in the tissues of embryo, juvenile and adult Spotted Salamanders (*Ambystoma maculatum*). An association between the alga (its species name means "associates with spotted salamander eggs") and salamander eggs had been recognized for well over a century (Orr 1888), but only with the advent of fluorescence and advanced electron microscopy did it become possible to demonstrate that the algae occur in the tissues of the salamanders. This discovery represents a confirmation of a Hypersea prediction. Hypersea analysis promises to help improve our understanding of terrestrial ecology and paleoecology in the decades ahead. Endosymbiotic photosymbiosis is of course better known in land plants, and cases such as the cycads (which have two types of endosymbiosis–native chloroplasts and the photosynthetic algae of their peculiar coralloid roots; McMenamin and Ulm 2004; Bergesen 1965) and loss of the *entire* chloroplast genome in *Rafflesia*, presumably due to its parasitic hypermarine lifestyle, are cases that cry out for further research.

12. Where fossils are rare, due to the strata being deposited shortly after a mass extinction or other factors, each fossil find is of potentially great significance. Use this observation as a guide to choosing new field sites.

Restating recommendation number one, the proper role of paleontology in the scheme of things is to solve the great unsolved problems. Three unsolved problems, above all others, command the attention of the scientific community. All three of these may be addressed by the methods of *Dynamic Paleontology*. The first involves whether there is or was life on Mars (Valdivia-Silva et al. 2016). The second concerns the origin of life (Williams et al. 2005). The third—arguably the most difficult of the tree—is what happened during the Cambrian Explosion. Why did the elaborate forms of the Early Cambrian, so different from one another and showing such a panoply of behavioral complexity and sophistication, appear so suddenly at the beginning of the Paleozoic Era?

Georgopoulos (1991) has shown that "changes in activity observed in central motor structures in tasks with visually guided movements do not relate exclusively to upcoming peripheral motor events (e.g., muscle contractions) but instead reflect higher order processing of visuomotor information." Thus, an apparently simple task in a metazoan such as muscular coordination requires complex higher order processing. If our hypothesis of the Triassic Kraken is correct, that would be astonishing enough, but the real cause for astonishment is the cognitive sophistication of the Early Cambrian animals (Yang et al. 2016). Indeed, one member of the fauna has even been called a "little Kraken" (Bengtson 2010)—the "presumably carnivorous" *Nectocaris pteryx* and allied forms have been identified as Early Cambrian cephalopods (Smith and Caron 2010).

The fossils occurring at the base of the Cambrian confront conventional evolutionary theory with a great challenge. Do they constitute a fatal stumbling block for theories of morphological evolution for which the natural selection of small changes over geologic time is postulated? Charles Darwin admitted in *Origin of Species* that the sudden appearance of complex animals was problematic for his evolutionistic schema. No surprise then that Darwin was the first scientist to rationalize away the abrupt appearance at the outset of the Cambrian with an appeal to the incompleteness of the fossil record. Darwin compared the rock record to a damaged folio volume, for which we have only a page here and a paragraph there.

Charles D. Walcott, who famously discovered the Middle Cambrian Burgess Shale fossils in British Columbia, Canada, attempted to address Darwin's difficulty by proposing the Lipalian interval—a vast stretch of geologic time not represented by strata. Walcott realized that a gap in the record could rescue Darwin's schema by providing a ready excuse for the missing ancestors. Field studies, however, have shown that many Precambrian–Cambrian boundary sections (McMenamin 1984; Stewart et al. 1984) show no evidence for such a profound gap.

In one of the great ironies in the history of science, Walcott's discovery of the Burgess Shale had a result diametrically opposed to his Lipalian gambit. Burgess creatures look distressingly modern (Bengtson 1986). Making matters worse, the mid–1980s discovery of Early Cambrian soft–bodied fossils of the Chengjiang biota (Xian-guang et al. 2004) in the Yunnan Province of China further compounds the problem. Chengjiang has produced fossils even more modern looking than those of the Burgess Shale, among them being the first fossil fish, *Myllokunmingia*. We can now fully appreciate that it is not merely the precursors of tetrapod (*Myllokunmingia*) and cephalopod (*Nectocaris*) intelligence that appear in the Cambrian Explosion, but rather their full manifestation albeit in rudimentary form.

Erwin and Valentine (2013) state that gene expression supposedly becomes "increasingly inflexible" because of the establishment of metazoan developmental kernels. Erwin and Valentine (2013) note that these kernels are "refractory to modification once they form." Their solution to this dilemma is to describe a combination of the advent of the *cis*–regulatory evolution of genome networks and an immutable codification of the developmental kernels. There is, however, evidence that *cis*–regulatory features and developmental kernels were already in place at a very early date. Ediacarans first appeared 585 million years ago (Kaufman et al. 2007). The Sonoran Ediacaran assemblage includes the oldest known chiton (McMenamin 2011).

This is a good opportunity to review the Sonoran Ediacaran assemblage, considering its key stratigraphic position. The community hosts the oldest diverse Ediacaran assemblage known in the fossil record (McMenamin 1996), and is thus critical for our understanding of the events leading up to the Cambrian Explosion. The assemblage occurs in the Clemente Formation, and contains six different types of body fossil and four different types of ichnofossil, not counting biofilm structures such as elephant skin textures. Both animalian and non–animal (vendobiont, petalonamid or rangeomorph taxa) body fossils occur in the Clemente Formation. Representing the former is *Clementechiton sonorensis* n. gen. n. sp., the oldest known fossil chiton. This fossil occurs in the same stratigraphic layer as do most of the other Clemente Formation fossils. With *Clementechiton* we have direct fossil evidence for a complex animal (Figs. 14.1, 14.2, 14.3, 14.4 and 14.5) at a very early date.

Chitons are interesting animals, as their shelly valves are covered with scattered tiny organs called aesthetes. It has recently been shown that chiton aesthetes serve as an enormous compound eye consisting of separated individual organs that nevertheless act in unision (Li et al. 2015). Thus the shelly plate scleritome of modern chitons multitasks as a visual system, a single gigantic eye.

Very interestingly, the mega–aesthetes of *Clementechiton* are clustered together in what appears to be a more conventional compound eye (Figs. 14.1, 14.2, 14.3,

Fig. 14.1 *Clementechiton sonorensis* n. gen. n. sp., intermediate or median valve from Unit 4, Clemente Formation, Cerro Rajón, at a stratigraphic position approximately 5–10 m beneath the Clemente oolite. Specimen of a single body valve dorsal external mold as seen in the matrix. Scale bar in mm; IGM 7461

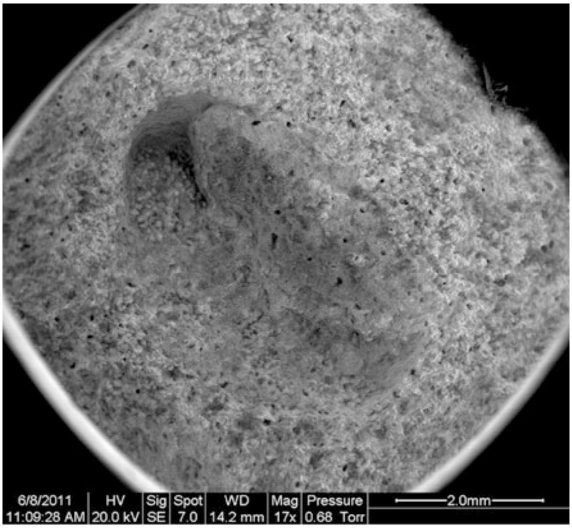
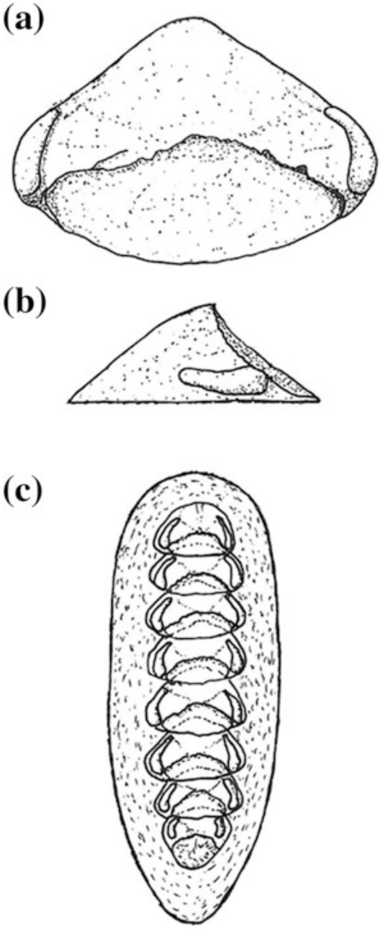


Fig. 14.2 *Clementechiton sonorensis* n. gen. n. sp. Scanning electron micrograph of intermediate valve of shown in previous figure. Scale bar 2 mm; IGM 7461

Fig. 14.3 *Clementechiton sonorensis* n. gen. n. sp. Reconstruction of single valve and the entire animal. **a** Intermediate valve, dorsal view, width of valve 4.2 mm; **b** Intermediate valve, lateral view; **c** Reconstruction of entire animal. Degree of valve coverage or overlap conjectural. Estimated length of body approximately 2 cm



14.4 and 14.5). Lest it seem odd that a mollusk could form a compound eye of the type more usually associated with the Arthropoda, the clam *Arca* sees with compound eyes positioned along the edge of its mantle (Waller 1980). The development of compound eyes represents a criterion example of convergent evolution (Conway Morris 2003), as it has appeared independently four times: in arthropods, in sabellid worms, in *Arca* bivalves, and now in *Clementechiton*. Dzik (2003) generated controversy (Zhang and Aldridge 2007) when he suggested that the *Microdictyon* sclerites (Figs. 1.8 and 1.9) were actually compound eyes (Dzik 2003), and that "even their homology with arthropod eyes cannot be excluded." Dzik (2003) may be correct, and if so, we may in fact have a fifth case of independent development of the compound eye, this time in the lobopodian *Microdictyon*. Whether or not the *Microdictyon* plates actually served as eyes (the case seems plausible considering the situation with chiton aesthetes), it seems certain that at the very least the *Microdictyon* trunk plates are torologous with compound eyes of other metazoa.

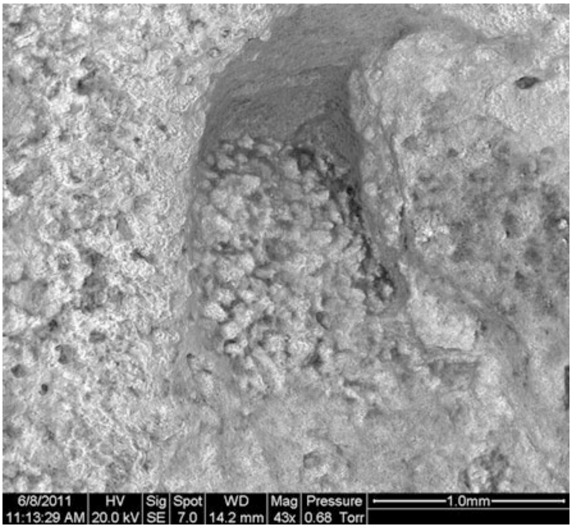


Fig. 14.4 *Clementechiton sonorensis* n. gen. n. sp. Scanning electron micrograph of aesthete–rich region on valve surface, showing polygonal tips of mega-aesthetes (preserved as fine sediment casts) and, on the *right* side of the image, conical and slightly *curved* mega–aesthete canals that are preserved on their side. Scale bar 1 mm

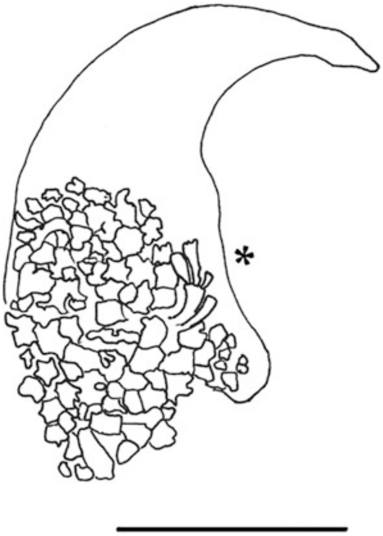


Fig. 14.5 *Clementechiton sonorensis* n. gen. n. sp. Line art sketch of mega–aesthetes as seen in the previous figure. Asterisk (*) indicates location of mega–aesthetes preserved on their sides, showing the *conical* shape of each tube. Scale bar 1 mm

We see here a potential corollary to Sbaglio's Law, where field vectors may on occasion be bundled or bunched in a geometrically regular fashion to generate compound eyes or their torologous scleritome equivalents.

As members of the Polyplacophora, the early chitons show that *cis*–regulatory networks and developmental kernels were already functional. In a key admission that amplifies the magnitude of the Cambrian Explosion, Erwin and Valentine state (2013) that there "simply may not be any viable phenotypic variation within the developmental kernels for selection to act upon." This presents us with a serious conundrum. Extant animal groups appear early in Ediacaran times, but somehow, the explosion proceeds without warning, evidently by processes that do not (or, if we believe in the rigidity of developmental kernels, cannot) require the agency of natural selection.

One particularly vexing aspect of the problem is that no new phyla can be shown to have appeared after the Cambrian (Valentine 1995), thus the origin of metazoa phyla presents a singularity that is difficult to study scientifically as it represents an isolated case. Some paleontologists thought that *Tullimonstrum gregarium* represented a new phylum that appeared in the Carboniferous, but recent research suggests that it is in fact a bizarre vertebrate comparable to lampreys (McCoy et al. 2016). No one can (yet) create a new phylum in the laboratory. For the last half billion years nature has "failed," or, if we may extend the anthropomorphism, "has been unwilling" to produce a single new phylum since the Cambrian.

Nevertheless, there may be a way to pry open this problem, crack the kernel so to speak, and take a peak inside the evolution engine. To do so, we must make a search for modern examples of anomalously rapid evolution. Could there be a group or groups out there that retain some hint of the Cambrian Explosion, possibly by virtue of some sort of morphogenetic reset that hints at the mechanism of the explosion event?

Their rows of scute plate armor and heterocercal tail impart to sturgeons a decidedly ancient look. Sturgeons are thought to first appear some time before 200 million years ago (Bemis et al. 1997), conferring on them "living fossil status" as they originate at approximately the time of the deposition of both the Luning (marine) and Portland (terrestrial/lacustrine) Formations, strata–of–interest in preceding chapters. Sturgeons are the oldest known type of actinopterygian (ray–finned) fishes. They appear in the Late Triassic as part of the Chondrostei subclass that includes sturgeons, paddlefishes, reedfishes and bichirs. Although they are bony fishes, sturgeons have evidently experienced a neotenous loss of mineralized bone.

Sturgeons vary widely in size. The beluga or European sturgeon (*Huso huso*) is the largest freshwater fish, reaching over 7.2 m in length and 1571 kg body mass. Rabosky et al. (2012) have detected very fast evolution in sturgeons with regard to body size, a rate 5.4 times faster than the average for fish lineages. Nevertheless, Rabosky et al. (2012) predict "that sturgeons will be characterized by low rates of body shape evolution relative to many other fish lineages." They write:

> The connection between speciation and morphological evolution is partly consistent with traditional formulations of punctuated equilibrium, whereby the speciation process itself leads to morphological change. However, an alternative explanation for this result is that phenotypic evolvability—the capacity of lineages to evolve morphological and ecological novelty—itself promotes speciation. Many biologists already recognize this notion intuitively as the mechanism by which ecological key innovations promote diversification during adaptive radiation.

This is paradoxical, with sturgeons showing rapid microevolution in terms of body size, but presumed slower than usual rates of macroevolutionary change in terms of body form. This does not bode well for any attempts to extrapolate microevolutionary change to explain macroevolutionary change, indeed, Russian scientists have argued that doing just this was Charles Darwin's biggest mistake (McMenamin 2003).

The sturgeon genome has a very unusual characteristic. Some researchers claim that it carries eight copies of the basic genome to render the creatures not merely polyploid but octoploid. Schreier (2014; 2011) notes that:

> White sturgeon may be evolutionary octoploids but are all eight copies of their genes expressed? Or have some extra gene copies been lost or silenced because they are no longer needed? Recent research on polyploid plants has documented high levels of duplicate gene retention and subfunctionalization (different gene copies operating in different places or different times) but no one has investigated this in a vertebrate animal.

Havelka et al. (2010) note that polyploidization "is closely connected with frequent interspecific hybridization events. At least twelve different types of interspecific hybrids and five intergeneric ones have been described" some of which are fertile, such as the *bester* hybrid. Havelka et al. (2010) affirm that due "to the unusual genetic structure of the acipenserids [sturgeons] they hybridize more easily than other vertebrates." Thus we observe odd genetic propensities in a major fish group that appears relatively late (Late Triassic) in the evolution of major fish types.

We may be able to detect here a link between genomic chaos, wide variations in body size, and what we might call "morphogenetic morphology." The armored nature of the sturgeon, morphogenetic field lines in full view along the scute rows, plus weird ploidy and massive interspecific variations in body size, provides us with an important clue. Other, unrelated organisms reveal facts of similar import.

Lake Baikal has the largest known freshwater amphipods, with some forms approaching 10 cm in length. Very interestingly, polyploidy has been detected in amphipods (Salemaa 2008). The Baikal genus *Acanthogammarus* is highly spinose, with presumably defensive spines that have been called "body teeth." Parker (2009) noted the remarkable resemblance between *Acanthogammarus* and a group of Triassic tetrapods known as the aetosaurs.

Aetosaurs are an exclusively Triassic group of archosaurs, and thus allied to the other archosaur groups such as crocodylomorphs, dinosaurs, and pterosaurs. Aetosaurs were first recognized by Agassiz (1844) in his description of the genus *Stagonolepis*. Agassiz (1844), however, had misidentified *Stagonolepis* as a fish (Huxley 1875). We may pardon Agassiz (1844) for his conflation of the osteoderms of an aetosaur with the scales of a large fish; indeed, this error points to an important insight. It was a mistake that, as has been said, was bursting with the seeds of its own correction. We now know that the similarities between the osteoderm armor of an aetosaur and the scales of a fish represent a case of torologous evolution.

Aetosaurs have a body plan that is covered with geometrically placed osteoderms (composed of a spongy bone type known as diploë), and these form anterior to posterior rows somewhat like the scute rows of sturgeons except that the aetosaur osteoderms are larger and fit together like mosaic tiles on the ventral and dorsal sides of the animal. Its body surface "scleritome" is described by precise terminology:

cervical paramedian plates, cervical lateral plates, dorsal paramedian plates, dorsal lateral plates, ventral plates, dorsal caudal paramedian plates, dorsal caudal lateral plates, ventral caudal lateral plates, and ventral caudal paramedian plates, etc. As aetosaurs represent a fairly early and underived ("primitive") archosaur type, they provide us with a clear example of the Second Law of Morphogenetic Evolution (McMenamin 2009), namely, that evidence for morphogenetic fields is most apparent in the earliest representatives of any particular animal lineage. This law applies to our own Hominidae lineage.

Penile spines in chimpanzees (*Pan troglodytes*) and other of our close relatives are linked with an apparently brutal aspect of great ape sexuality; the spines rip up the female so that she forms a mucus plug that will block the sperm of the next incoming male. The loss of this penile 'scleritome' in *Homo sapiens* radically altered the fundamental mechanics of human sexuality, and has been linked to monogamous relationships in humans (McLean et al. 2011). Vestigial remnants of penile spines develop in some human males, and are called pearly penile papules (*Hirsuties conorae glandis*). McLean et al. (2011) argue that a highly conserved DNA region (hCONDEL) near the androgen receptor gene locus contains deletions that led to penile spine loss in *Homo sapiens*; however, there is still weak expression of this 'scleritome' in some individuals, thus a morphogenetic field explanation for the elimination of the penile spines is considerably more likely and it may also help explain any correlations between loss of penile spines and loss of body hair.

Aetosaurs develop "body teeth" and an overall body form that is remarkably similar to that of the acanthogammarid amphipods of Lake Baikal (Sherbakov et al. 1998). Sherbakov et al. (1998) conclude that in the Baikalian amphipods, some "important morphological characters appear independently in both lineages and suggest parallelism in the development of gigantism and body armament." Here again we see torologous convergence. Variations in body size may thus be regarded as torologous inflation or deflation of the torus, respectively. If inflation is faster in the mid–region of the animal than at its anterior and posterior ends, new sclerites or new sclerite rows may need to be added. This would represent the promotion (or intercalation) of second order field lines to what would effectively serve as first order morphogenetic field lines. The relationship between sclerite rows and underlying metameres in *Wiwaxia* is necessarily imprecise (Yang et al. 2014); the later is controlled primarily by the nuclear genome, whereas the former is largely controlled by the morphogenetic field. This same distinction holds for the mismatch between spider metameres (such as the abdomen/opisthosoma and cephalothorax/prosoma) and the coloration pattern of European Black Widow (*Latrodectus tredecemguttatus*) as seen in Fig. 1.7.

The Baikal amphipods such as *Acanthogammarus* develop shoulder spikes and a dorsal armor that bear striking similarity to the shoulder spikes of aetosaurs, which are derived from the dorsal eminence of the anterior lateral plates. The "body teeth" of acanthogammarids and aetosaurs are torologous, in other words, the similarities are neither superficial, nor an ordinary case of convergent evolution, but rather a shared evolutionary trajectory that derives from the common, and held in common, toroidal morphogenetic field.

Let's apply this analysis to another archosaur group, the ornithischian dinosaurs. These "bird–hipped" dinosaurs include the thyreophorans (stegosaurs and ankylosaurs), the iguanodontids and the ceratopsians such as *Triceratops*. Ironically, birds are descended from the "lizard–hipped" saurischian dinosaurs. Torological comparisons between the ornithischians and the aetosaurs are evident, such as the dorsal armor and shoulder spikes of the ankylosaurid *Edmontonia*. The enormous shoulder spikes of the stegosaurid *Kentrosaurus* confirm the pattern. Stegosaurs in general show an emphasis on the dorsal morphogenetic field with their double row of plates along the dorsal midline and prominent tail spikes, also in rows.

I predict here that thyreophorans and aetosaurs will be shown to have carried larger genomes, perhaps to the extent perhaps of having been polyploid. Already we see that ornithischian dinosaurs had larger genomes than the flying saurischians (birds), with the latter being more genetically "streamlined" (less DNA, smaller cells) to satisfy the metabolic demands of flight. A recent estimate (Organ et al. 2007) holds that mobile genetic elements (repetitive DNA) constituted 5–12% of saurischian dinosaur genome size but 7–19% of the ornithischian dinosaur genome.

We see then that in many potential post–Cambrian echoes of the Cambrian Explosion, there may be changes to genome size up to and including polyploidy. Also, the morphogenetic field in these cases can become oddly emphasized: sturgeon scute rows, *Kentrosaurus* shoulder spikes, ceratopsian horns, and giant Baikal amphipods with body teeth.

The essential conclusion we may derive from this is that there are limits to post–Cambrian reconfiguration of animals. The Cambrian Explosion itself fundamentally involved simultaneous changes to the genome *and* to the morphogenetic field. The post–Cambrian genome might on occasion be subjected to what at first glance may appear to be radical change (chromosome duplication, polyploidy), but the genomic kernel remains unscathed and although animal size may be greatly inflated or contracted, and the morphogenetic field can enhance or even revive (Yang et al. 2014) the scleritome without notice (recall the saurischian titanosaurs) giving rise to bony scute rows, prominent torologous spikes and torologous projections, apparently nothing can fundamentally alter the core metazoan baüplan.

The scientific singularity of the Cambrian Explosion thus remains unexplained. Explanations that argue that the big changes resulted from a wide-open, less competitive environment are inadequate to the task. I suspect that, during the Cambrian Explosion event and *only* during that event, changes to the morphogenetic fields were primary, and that the genome was modified in response, or that in some currently unknown fashion the two were changed in concert. Could torologous nudges to the morphogenetic field somehow lead to a fundamental genomic reset? If so, the usual rules of evolution would be turned on their heads. Instead of the genome changing and then being selected upon as new morphologies were generated and tested in the wider environment, morphologies would instantly appear in a spasm of torologous changes at small size, early in development.

This begs the question of what was the external agency that caused the simultaneous reconfiguration of so many metazoan genomic kernels? I propose here that the agent took the form of a torologically and genomically active virus with access to the kernel. Let's call this the Cambrian Explosion virus or *CE virus*. The CE virus triggered an extreme type of somatic transformation cascade quite apart from viral oncogenesis. Its action might be described as a viral reconfiguration of the entire metazoan construct at the zygote or germ cell stage. The syndrome that resulted in infected embryos is referred to as virally–induced pleomorphism. Several types of bacteria (Wainwright 1997; Joshi and Toleti 2009; Andersen and Rasmussen 2009) and viruses themselves are known to undergo pleomorphism, so what is being hypothesized here is a short–lived episode of virally–induced pleomorphism in early animals that led to the sudden appearance of new phlya.

The CE virus was able to infect something like *Clementechiton* and transform it into something like *Sprincrinus* in a single step or series of short steps. Indeed, the transformation from a protostome such as a chiton to a deuterostome such as an echinoderm (or vice versa) *had* to have taken place quickly, because their alimentary systems (guts) run in opposite directions. One's gut has to run in either one direction or the other, and there are no viable intermediates between the two states. So much for gradualism.

The CE virus must have been highly infectious, able to infect a variety of metazoa living in late Ediacaran times. It then went extinct shortly after having caused the Cambrian Explosion. The CE virus, presumably a rogue collection of metazoan DNA (but there are alternatives as discussed below), destabilized the kernel in a sublethal fashion that allowed a new phylum to "auto–configure" via pleomorphism in short order. Note that this hypothesis proposes that the virus can reconfigure the entire kernel; this is not just a modification of *Hox* or *Ubx* genes (Martin et al. 2016) to alter limb structure nor Delta/Notch signaling to modify segmentation (Janssen and Budd 2016), but something much more profound. The hypothesized destabilization event must have had the character of a serial endosymbiosis event, with some sort of directed genomic fusion that was repeated numerous times generating separate clades during the viral epidemic. Note that this concept is quite in accord with our current state of knowledge regarding viruses and their hosts combining genetic information (Shackelton and Holmes 2004), and the link between non-gradual evolution and extensive genomic remodeling (Jachiet et al. 2014).

Recall the discussion in Chap. 3 regarding the bizarre flat archaeocyath *Retilamina*, where it seems as if the morphogenetic field has gone out of control, penetrating deep into the interior of the animal rather than existing as a mere surface patterning grid. Is there a morphological and developmental relationship between *Retilamina* and Phylum Porifera, the sponges? Sponges have skeletons built up of spicules, and special biomineralizing cells called sclerocytes form these spicules. Although a number of sponge–like fossils occur in Proterozoic strata, the oldest undoubted sponge fossils are from the Lower Cambrian. One of the earliest of these (McMenamin 2008) is the sponge genus *Kiwetinokia*.

The evolution of spicule morphogenesis in the Cambrian sponge genus *Kiwetinokia* represents a departure from the rigid control of morphogenesis by a morphogenetic field. The expression of cell–cell adhesion (ADH/DAD) dynamical patterning module (DPM) effects *decreased* over time in the *Kiwetinokia* lineage. This particular deconfiguration had survival value in a Cambrian biosphere that favored filter and suspension feeders utilizing a mesenchymal body plan. This result is consistent with indications that sponges derive from a metazoan ancestor bearing the developmental toolkit for complex tissue grade multicellularity, and that this ancestral form was also the common ancestor of bilaterian metazoans. Cell–cell adhesion dynamic patterning modules are essential for animalian multicellularity (Newman and Bhat 2008; Newman et al. 2009). Cadherins (a major class of membrane proteins) execute the cell–cell adhesion dynamical patterning module (DPM), a dual module that consists of ADH (adhesion) and DAD (differential adhesion) effects.

Figures 14.6 and 14.7 show the earliest known representative (Botomian Age, Early Cambrian) of the sponge genus *Kiwetinokia*. It belongs to a group known as the protosponges. The specimen shows twisted spicule morphology (McMenamin

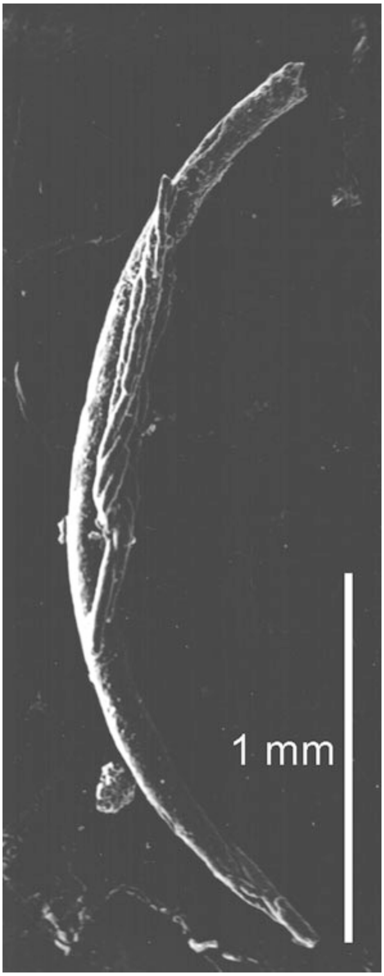


Fig. 14.6 *Kiwetinokia* sp. Several twisted and fused spicules are visible. Early Cambrian. Lower Unit 3, Puerto Blanco Formation, Cerro Clemente, Sonora, México, 1 of 12/15/82; modified from McMenamin (2008). Scale bar 1 mm

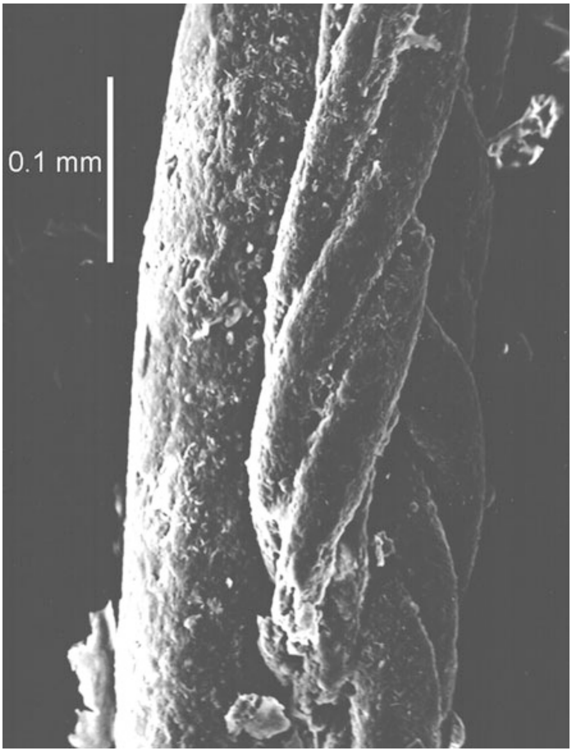


Fig. 14.7 *Kiwetinokia* sp. Enlargement of the twisted spicule cluster seen in previous figure. Scale bar 0.1 mm

2008). Continuous cell motion characterizes modern sponge morphogenesis (Bond 1992). In *Kiwetinokia* sp., spicular twisting indicates that the sclerocytes responsible for each spicular strand adhered to, and simultaneously twisted around, neighbor sclerocytes in clusters of two, three or even more cells to form the spiraling spicular bundle. Later Cambrian species of *Kiwetinokia* (such as Middle Cambrian *Kiwetinokia spiralis*) also show twisted spicules, but the bundles have fewer strands, involving only a single pair of sclerocytes. This implies that over the course of the Early Cambrian, the genus *Kiwetinokia* reduced its expression of ADH and DAD DPMs in several species–level phylogenetic steps on a trajectory leading *away* from complex tissue–grade multicellularity. In other words, these sponges were driven away from somatic control by some process that was in a way comparable to carcinogenesis. The degree of integration was much less than in a typical metazoan, and it is as if the integration function has been "damaged" or modified, possibly by the influence of the CE virus. This somatic disintegration reaches its maximum expression in the glass (hexactinellid) sponges. These sponges lose individual cell membranes and become syncitial, with cell nuclei swarming in a mass of cytoplasm. The syncitial habit, more characteristic of amorphous organisms such as slime molds, is very unusual for animals.

The evolution of spicule morphogenesis in *Kiwetinokia* represents a phylogenetic analogue to the epithelial–mesenchymal transformation (EMT) known in cnidarians (jellyfish and their kin) and triploblastic bilaterians. Reliance on the ADH/DAD dynamical patterning module was reduced in a departure from the primarily epithelial format of typical, bilaterian metazoans. *Kiwetinokia* simultaneously amplified its reliance on the extracellular matrix (ECM) dynamical patterning module, thus constituting a shift to a body plan with an increasingly mesenchymal format. Modern sponges are thoroughly mesenchymal organisms that depend heavily on the ECM.

This inference of an epithelial to mesenchymal body transformation gains credence from the fact that sponges have homologues of basement membrane type IV collagen (Boute et al. 1996; Nichols et al. 2006) and epithelial cells (Schröder et al. 2004), which both thereby take on a vestigial aspect in sponges. This is in accordance with the hypothesis that parazoans (sponges) and metazoans (all other animals) share a common animalian ancestor that had epithelial cells, basement membrane type IV collagen, and cell–cell adhesion DPMs. *Kiwetinokia* eliminated rigid cell-cell adhesion dynamical patterning module effects through the Cambrian, in essence unraveling its morphogenetic field, even as such effects were elaborated along with other DPMs in bilaterally symmetric, complex animals such as trilobites. Parazoan animals (such as sponges) should be seen as highly successful variations on "ur–metazoan" morphogenesis, optimized for suspension and filter feeding in a Cambrian marine biosphere that favored such feeding strategies, with new food sources being introduced into the water column by burrowing–induced fragmentation of the biofilms. Sponges subsequently reduced the epithelial format of their body plan even further by introducing intracellular spicule formation within epithelial cells (Maldonado and Riesgo 2007). The sponge morphotype has fewer morphogenetic possibilities than essentially epithelial organisms such as Cnidaria (jellyfish and corals), or than the triploblastic bilaterians, which owe their morphological complexity to organization of epithelial and mesenchymal tissues by morphogenetic field patterning.

Sponges represent a radical modification of morphogenetic field control of body form. Archaeocyaths, on the other hand, represent animals at or near the sponge (parazoan) grade of organization that submitted to developmental control by a still largely toroidal morphogenetic field. The riot of new archaeocyath species and genus level evolution in the Early Cambrian results from the deconstruction of a metazoan morphogenetic field to a less–structured parazoan morphogenetic field. This evolutionary event deserves its reputation as the greatest single blast of the Cambrian Explosion. It is frankly weird, and may also provide evidence for the influence of the destabilizing CE virus.

This deconstruction of the metazoan morphogenetic field and the loss of cell–cell adhesion ("stickiness") in an early sponge poses a serious stumbling block for the concept that the Cambrian Explosion was the result of increasing levels of atmospheric and aquatic oxygen. This vintage idea (Nursall 1959) has subsequently been linked to the appearance of oxygen and to the development of metazoan collagen (Towe 1970), the development of cell adhesion (Saul and Schwartz 2007), and the appearance of predators that fed on other metazoans (Sperling et al. 2013). However, oxygen levels varied widely over Proterozoic time and thus the fact a major group (parazoans) lost cell stickiness at the same time as the occurrence of an explosion of phylum–level metazoan evolution poses a serious problem for the oxygen hypothesis. It does not seem plausible that increased ambient oxygen could have caused *both* the simultaneous emergence of complexity in metazoans and the "demergence" (Sonnenschein and Soto 1999) of complexity in sponges.

Sequelae of the reconfiguration that led to archaeocyath body form are seen in the contrast between a cup and wall structure that is geometrical in the extreme, versus the cancer–like exothecal adventitious growths that are often seen growing out of archaeocyath skeletons. These are disorganized and tumor like in form. The morphogenetic dissonance led to a feedback in archaeocyath morphology, and accelerated the rate of new genus and species production to a level that has never been seen before or since. It is as if the "generate species" knob is stuck on fast forward, producing in short order a kaleidoscopic explosion of archaeocyath body form that lasts until an extinction event later in the Cambrian. Are the exothecal outgrowths a variant of cancer ('meta–morpho–cancer') that is correlated to the extremely fast genus–level diversification in archaeocyaths?

If typical animals represent the metazoan grade of organization, and sponges the parazoan grade of organization, the archaeocyaths then represent an "archaeozoan" grade of organization that is intermediate between the metazoan and parazoan grade. The peculiar archaeocyath body plan and the sudden appearance and lightning fast diversification (fast even by Cambrian Explosion standards) share the same cause. That cause is megaviral destabilization, and concomitant morphogenetic field destabilization of the animalian constitution, beginning with a presumably conventional if underived metazoan form, and reconfiguration in a new phylum or even superphylum (archaeozoan) grade manifesting an intermediate level of weakening of the dynamic patterning modules associated with cell adhesion. *Retilamina* takes this a step further, being the archaeocyath that attains the parazoan (sponge) grade of organization by abandoning even a hint of toroidal metazoan body form. In a typical cup–shaped archaeocyath, the central cavity (Fig. 3.1) is thus homologous to the metazoan gut. By transitioning from metazoan grade to archaeozoan grade to parazoan grade, the sponge or parazoan grade was attained by virally–induced convergent evolution at least twice (hexactinellid sponges, *Retilamina*) during the Cambrian Explosion.

The virus must have had both a genomic and torologous effect, thus Sbaglio's Law would still apply, as the CE virus was involved in reorienting all morphogenetic surface field vectors. This would be comparable to a modern virus that has both "nuclear and cytoplasmic replication stages" (Priet et al. 2015). It is consistent with Carroll's (2005) claim that evolution occurs at two levels: genes and form. Both were driven to extreme restructuring and that is what generates the Cambrian Explosion. The second law of morphogenetic evolution (McMenamin 2009) is reset at the morphogenesis events, thus "primitive" morphogenetic fields are present in most of the early representatives of the new phlya. Once again, the really astonishing thing about the Cambrian Explosion is the speed of the event. The transition from, say, from the ventral nerve cord ground pattern in the Panarthropoda to the independent secondary losses in both tardigrades (water bears) and euarthropods (familiar arthropod types) of cycloneuralian–like neurological features (Yang et al. 2016) suggest that the transformation in the two groups occurred so quickly and simultaneously that an external agent such as the CE virus was necessary to provoke the observed rapid change.

The particular pathology of this CE virus may have had to do with a targeted disruption of the morphogenetic field, and thus it may also have had a cell membrane replication stage. If so, then it may truly be reiterated that the field lines *lead*, and the genome *follows*. The CE virus must have had a close resemblance to, or even an ancestor–descendant relationship with, animalian maternal RNA in order to have such a profound effect on the morphogenetic field. Lee et al. (2013) calculate that the rate of evolution during the Cambrian Explosion was five times faster than usual, but this estimate is too low. Their calculation runs afoul of the sampling bias as per the Lignor–Sipps effect. The Cambrian Explosion is far too rapid for any sort of gradualistic, or even accelerated gradualistic, evolutionary change.

Erwin and Valentine (Erwin and Valentine 2013) were quick to realize the problem that a fast Cambrian Explosion poses for explanations of the event that rely on "traditional microevolutionary processes." These same authors had earlier (Erwin and Valentine 1984) argued that "RNA–based viral transfer of transposons [transposable genetic elements] among members of a population suggests novel, potentially nonrandom, methods of producing genetic variability, simultaneously transferring the changes to other members of a population." Erwin and Valentine (1984) thus addressed a novel way of producing variation, and at the same time proposed a solution to the hopeful monster problem, namely, if a bizarre macroevolutionary variation appears in a single individual, who is this hopeful monster going to mate with? The hopeful monster problem, however, is not actually as serious as it first may appear, because there are ways around the apparently insurmountable difficulty by hybridization, parthenogenesis, asexual budding following by spontaneous sex changes, etc. Perhaps caught up in the current enthusiasm for "ecosystem engineering"–style explanations, Erwin and Valentine (Erwin and Valentine 2013) do not even cite Erwin and Valentine (1984). In invoking viruses, Erwin and Valentine (1984) were on the right track, although their main argument in that article was that retroviruses could insert genes as specific points in the genome, thus creating 'like' mutants and eliminating the hopeful monster conundrum. It was indeed a speculative scenario, and Erwin and Valentine (Erwin and Valentine 2013) probably rejected it because, although it helps to render the Cambrian Explosion fast, it cannot address the necessary restructuring of the metazoan genomic kernel, disturbance of which is always fatal and as Erwin and Valentine (Erwin and Valentine 2013) admit, cannot as a consequence be subjected to natural selection (McMenamin 2013). The CE virus hypothesis differs greatly from the hopeful monster transposon hypothesis, as it requires a complete reconfiguration of the genome, including the genomic kernel, not just a gene insertion here or there. Erwin and Valentine (1984) were correct in their hopeful monster transposon paper to emphasize the abrupt nature of the Cambrian Explosion and the difficulties that it poses for "traditional microevolutionary processes."

The spread of the CE virus was facilitated by the extreme environmental disruption caused by the breakup of the biomats in the transition from stromatolitic biofilm marine biosphere to metazoan marine biosphere. Its spread might share characteristics with the contemporary spread of the maternally–transmitted and sexually–transmitted Zika virus that has been implicated in fetal development abnormalities (Mlakar et al. 2016; Oliveira Melo et al. 2016; Fauci and Morens 2016). The virus was enzootic to the early metazoan fauna, members of which were at the time not too distant in terms of their phylogenetic separation. Their toroidal machinery was similar enough at the time to be susceptible to CE viral infection. It is likely that a viral explosion was simultaneous with the metazoan Cambrian Explosion. Some of these viruses may have been able to infect protists and other types of non–animal eukaryotes.

The CE virus shared some properties with modern oncoviruses that are able to infect more than one species. The common cold virus (adenovirus) in humans is known to be able to infect the Syrian or Golden Hamster (*Mesocricetus auratus*) and other rodents, where it acts as an oncovirus generating virus–induced cancers. Hamsters are a favored animal model in a search for oncolytic (tumor–destroying) andenovirus of potential use for cancer treatment in *Homo sapiens* (Thomas et al. 2006).

Oncogenes have been proposed as having a causal relationship to the Cambrian Explosion (Davidson et al. 1995; Conway Morris 2000). This suggests that the CE virus may have been carried by an asymptomatic metazoan species, now extinct, that at the time of the Cambrian Explosion served as a nidus (natural reservoir) for the CE virus. Able to infect other metazoan species, the CE virus would presumably infect all the cells of the host and thereby reach the unfertilized eggs where the hypothesized morphogenetic–genomic transformation would occur. The CE virus overcomes the hopeful monster difficulty by hybridization, parthenogenesis, asexual budding followed by spontaneous sex changes, or some other factor. Like an immunosuppressive virus today, the CE virus was somehow able to bypass the ordinary constraints of the genomic kernel, reconfigure the genome, and as a byproduct facilitate hybridizations among cohort mates that might not ordinarily be viable.

A potentially very interesting question is whether or not this viral transformation had a parthenogenetic reproduction aspect. Virally–induced parthenogenesis has not been reported in the wild, however, the *Wolbachia* microbe has been linked to parthenogenesis in infected insects (Weeks and Breeuwer 2001). With regard to the action of the CE virus, we must consider the scenario. A female metazoan gravid with unfertilized eggs is infected with CE virus, and all of her eggs are also infected via maternal transmission. Parthenogenesis then takes place in each egg, in concert with morphogenetic–genomic restructuring. The viral infection attracts (or perhaps substitutes for) maternal RNAs to the egg cell surface at the point of entry (just like a sperm) and a morphogenetic field appears in a fashion analogous to its appearance after the ordinary fertilization event. The virally– induced morphogenetic–genomic restructuring process is unique to each infected egg, thus, when the mother gives birth, she has the potential to give birth to a number of nascent phyla equivalent to the number of eggs she carries. This represents a variant on the concept that a single Late Proterozoic species "could have been the ultimate ancestor of more than one phylum" (Saul and Schwartz 2007). This of course does not guarantee that each reconfigured offspring will be viable. Indeed, this would be unlikely to be the event considering the profound nature of the transformation in each egg cell. Graham (1992) argues that these unsuccessful variants would be lost to "cancer selection" as numerous fatal juvenile cancers would be the price of a sudden increase in organismal complexity. The survivors would be new phyla. Let's consider the possibility that transmission of CE virus was mother–to–child. Infection of a single cell zygote (or egg just prior to fertilization) would cause heritable changes to the maternal RNA–derived (Schier 2007) morphogenetic field and the metazoan genomic kernel of the embryo. This would represent an extended maternal effect (Mousseau and Fox 1998), already known to be an important factor in phenotypic plasticity.

Interestingly, Stéphanie Priet et al. (2015) state regarding the Mimivirus: "We hypothesize that the second gene of the cluster … could play the role of the ruler through its specific interaction with the RNAse and the RNA … All members of the mimiviruses sub–family encode a mRNA capping enzyme also performing the N7 methylation of the cap … Hairpin structures–based processes have been documented in the cellular [i.e., eukaryotic] world for RNA maturation … [the] viral enzymes are reminiscent of cellular ones … *Pithovirus sibericum*, a 30,000 year old virus revived from permafrost, although not a member of the Mimiviridae, also possesses an AT–rich genome and obeys the hairpin rule for its transcripts maturation." In order to win the battle for the host cell translation apparatus, Mimiviruses use eukaryote–like processes to stabilize their own mRNA while evidently engaging in host "cellular mRNA degradation (p. 12)." Thus we see, with these giant viruses, that they have eukaryotic cell–like RNA maturation processes and may be able to simultaneously degrade host mRNA while stabilizing their own. It seems then reasonable to infer that, immediately after egg activation in the body of a CE virus–infected mother, CE viral mRNA could substitute for degraded maternal mRNAs and thus take control of the embryonic morphogenetic field, likely in combination with nuclear viral genome replication after maternal transmission to the embryo. For externally fertilized eggs, the virus would infect the egg itself either before, during or after fertilization.

A dual genomic fusion would not be out of the question, and occurring at so early an embryonic stage the result could very well be profound genomic–morphogenetic reconfiguration combined with an aspect of instant symbiogenetic synthesis, so great an act of gene splicing that it negates the genomic kernel limitation. Some of the code in the large virus is dedicated to keeping the host alive throughout the reconfiguration trauma. When this succeeds, the next generation of virion is the next generation of reconfigured animal. The two are inextricably linked by near–instantaneous virus–induced 'phylum–genesis'.

The adept CE virus was thus a girus (giant virus; Etten et al. 2010) of the types (Mimivirus, Mamavirus, Moumouvirus, Terra, Pandoravrus, Pithovirus, Megavirus) all discovered within the last decade and currently known to infect amoebas such as *Acanthamoeba* and a few other types of unicell eukaryotes. The CE virus was then also member of the nucleocytoplasmic large DNA viruses (NCLDV), the collective to which gigantic viruses belong. Some researchers argue that the NCLDV, and possibly this might apply to the CE virus as well, may have incorporated very ancient and unusual genetic material unrelated to the DNA sequences of familiar types of organisms (Dickey Zakaib 2011).

The Mimivirus (0.6 μ across; so large that it was once mistaken for a bacterium) has a pentameral star structure on its outer capsid that recalls the pentameral symmetry of the echinoderm body plan. The Pandoravirus is even larger, reaching one micron across. But the Pithovirus is largest of all, reaching an enormous 1.5 μ, larger than many bacteria. These giant viruses have properties not observed in other, smaller viruses, including the ability to be infected by parasitic viruses known as virophages (La Scola et al. 2008). In the debate over whether or not viruses are alive, this new evidence has shifted the discussion in favor of viruses as life forms (Pearson 2008). The giant Pithovirus, *Pithovirus sibiricum* (reaching up to 1.5 μ, the largest known virus in terms of physical dimension), has been revived from 30,000-year-old Siberian permafrost (Legendre et al. 2014). This astonishing development, actual recovery of a paleovirus, demonstrates that certain parts of the fossil record are still alive. Research currently underway studying the life history and virulence of megaviruses should provide information critical for understanding the CE virus.

The CE virus may have reconfigured itself like a mutating HIV virus as it set to work reconfiguring the morphogenetic grid network and genome of the zygote. Viral replication became immediately and obligately symbiotic, with the viral genome permanently ensconced in the genome of the reconfigured host. The remains of this genome present an important research opportunity for the emerging science of paleovirology, a new discipline that searches for "fossil DNA," regions of endogenous viral elements (EVEs) ensconced in living genomes (Weiss 2006). The process gives new meaning to the phrase corporate takeover, as the virus constructed a radically new metazoan with the potential to become extremely successful and abundant. Some species of infected metazoan served as nidus to produce viral propagules that could infect other metazoan lineages.

What was the nature of this invading genome? It may very well be associated with the genes that encode for the Pax6 (paired box) proteins in metazoans that are critical for development of the early embryo. The Pax6 gene family excercises control over the ectodermal region of the animal, and thus influences the morphogenetic field at the animal's outer surface. Pax6 genes are also critical for the development of the central nervous system and eyes (Walcher et al. 2013; Gehring and Ikeo 1999), both of which underwent major expansion during the Cambrian Explosion. The strange, eye–like (if not acutally eyes) trunk sclerites of *Microdictyon* (Dzik 2003) must surely have been influenced by Pax6, along with the compound and lens eyes that also first appear during the Early Cambrian.

The same is true for chitons, where tiny 'eyes' are dispersed over the scleritome or clustered together as in *Clementechiton*. Pax6 is also involved in cytoskeletal organization and is noted for its important role in brain development (Yamasaki et al. 2001).

The cactus–shaped Early Cambrian metazoan *Chancelloria* has a vase–shaped skeleton composed of distinctive star–shaped sclerites called coelosclerites (Bengtson 2004). *Chancelloria's* spongelike body form contrasts with its presumed coelosclerite–bearing relatives, who have sluglike bodies. *Chancelloria* apparently represents a case of Pax6 perturbation where what in related forms represents a dorsal sclerite field now wraps around the entire midline (dorsal and ventral) of the animal to complete the spiny scleritome that is torologous to spicules of a sponge skeleton. Any light sensitivity in *Chancelloria* coelosclerites has been lost or greatly limited, as these hollow spicules form as non–accretionary mineralization over the soft tissue that constitutes the core of the sclerite (Bengtson 2004). This is in accord with a presumed sessile, filter feeding benthic habitat of chancelloriids.

The vendobiont/petalonamid Ediacarans such as *Rangea* were evidently immune to CE virus, in accord with the concept that they were phylogenetically distant from true metazoans of the Ediacaran biota and subsequent Cambrian Explosion. Ironically, this eventually resulted in petalonamid demise as they could not compete with the panoply of aggressive new animals with restructured morphologies and reconfigured genomes. New ecological opportunities abounded and Cambrian ecosystem engineering proceeded apace. Similar ecological opportunities were available after the Triassic extinctions, however, and this is an important point, no new phyla appeared during the Jurassic. Presumably the reason for this is that the CE virus was no longer extant and no longer available to trigger macroevolutionary change as the nidus had gone extinct.

Extinction of the CE virus explains why no new phyla appear after the Cambrian. New higher taxa can appear in subsequent evolutionary radiations, but the CE virus is absent so new phyla cannot appear in these diversification events. Actinopterygian fish (Late Triassic) and amphipods (Eocene) represent major new types within their respective groups (bony fish and crustaceans, respectively), but these are not phylum grade appearances. An interesting task for genetic engineers would be to design an artificial analogue to the CE virus that can accomplish nonlethal destabilization of the metazoan genomic kernel and maternal RNA morphogenetic field and generate, in a single step, a new animal phylum. If this can be done, the artificial phylum thus created will be the first new phylum on Earth in well over a half billion years.

Reconstructing the CE virus may not be as daunting a task as it might at first appear, unless the viral genes have been completely cleared from all of the descendants of the Cambrian–emerging phyla. Modern marine viruses are poorly understood. A descendant of the CE virus may still be alive in the ocean or elsewhere, although of course not producing new phyla today as far as we know. As Jonathan Eisen put it in his attempt to detect new types of marine viruses by searching for unusual gene sequences in sea water: "I would call it the dark matter of the biological universe … There is potentially enormous diversity out there."

Much like the cosmic background radiation that provides us with evidence for the occurrence of the Big Bang, there are likely to be bits of the CE virus still extant in the genomes of the various metazoan phyla descended from the Cambrian Explosion event. A top priority for the biological sciences is to identify and sequence these bits. If this research program succeeds, it may not be necessary to synthesize a synthetic CE virus *de novo*, for there will be clues to its makeup residing in the genomes of most or all living metazoan species including our own.

It was initially thought that large viruses only infected amoebae until the giant virus *Marseillevirus* was identified in the swollen lymph nodes of an eleven–month old boy. The boy was declared cured one year later (Popgeorgiev et al. 2013). The leader of the research team, virologist Christelle Desnues, remarked that: "It is clear that giant viruses cannot be seen as stand–alone freaks of nature. They constitute an integral part of the virosphere with implications in diversity, evolution and even human health." The hypothesis presented in this chapter is that giant viruses *fabricated* stand–alone freaks of nature, namely, the new metazoan phyla that appeared during the Cambrian Explosion.

We can now answer the question posed by Bengtson (1991) regarding the origin of phyla—was it parallel or serial?:

> The two possibilities correspond to two evolutionary models for the origin of phyla: a parallel and a serial one. The parallel model implies that most of the phyla evolved their anatomical characters independently, by additions to a simple metazoan ground–plan. The serial model says that phyla evolved through successive branching from an limited number of lineages. The parallel model implies a large number of early phyla, whereas the serial model does not.

Arguments hinging on the idea that analysis of, say, Cambrian arthropod–like forms (Briggs et al. 1992) shows that they are not too distantly related, and thus disparity is less than some might think that it was during the Cambrian Explosion, are beside the point because this contention does little to bridge the gap between say arthropod and echinoderm. As there is insufficient time for successive branching, and the refractory nature of the metazoan genomic kernel would not allow this anyway under ordinary circumstances, and due to the fact that the CE viral restructuring was roughly simultaneous in the lineages that were thereby modified, Bengtson's parallel model is best supported by the available evidence. Bengtson's (1991) inference that the parallel model implies a large number (perhaps twice or more the 30–40 phyla existing today) of early phyla seems correct, although many of these were not long–lived and were lost to background or mass extinctions, especially during the end–Permian and end–Triassic mass extinctions.

In summary, the CE virus hypothesis provides the best (indeed, *only* scientific) explanation for the hardest–to–explain aspects of the Cambrian Explosion, namely, the morphological stasis in the wake of the Cambrian explosion (Yang et al. 2014), the phylogenetic telescoping seen in many lineages, and the basal polytomy (Mounce and Wills 2011) of lineages and the fact that so many phyla emerge so suddenly. There is a certainly some sort of phylogenetic continuity across the Cambrian boundary—*Vaqueroichnus stewarti* n. ichnogen. n. isp. may very well be the distant ancestor of the microburrow nest tracemaker—but this is one of the very few potential phylogenetic links that can be traced back to animal origins. Destruction of Microbial Mat World is more the result than the cause of the Cambrian Explosion.

Phylogenetic telescoping is not so much actual phylogenetic telescoping as it is geologically instantaneous viral generation of numerous new phylum–grade newcomers that would be considered 'stem forms' if considered separately. Many of the newcomers shared a common parent species, but each had its genome and field configuration destabilized and reconstituted in a unique way to generate a novel body plan. The CE virus provides macroevolutionary variation in a single step, in what could also be considered a sudden spasm of torologous convergent evolution. At last we can satisfactorily answer Harry Whittington's questions (McMenamin 2010) about the abrupt nature of the Cambrian Explosion.

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Systematics

Nature is very efficient at getting rid of its corpses.
Paul Olsen

Repository abbreviations are as follows: Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts, USA; Institute of Geology Museum (IGM), Departmento de Paleontología, Instituto de Geología, Cuidad Universitaria, Delegacíon de Coyoacán, 04510, México, D.F.; North Carolina Museum of Natural Science (NCSM), 11 West Jones St., Raleigh, North Carolina; Mount Holyoke College Paleontology Collection (MHC), Department of Geology and Geography, Mount Holyoke College, South Hadley, Massachusetts, USA; Smithsonian Institute (USNM), Washington, D.C., USA.

Systematic Ichnology

Ichnogenus *Helminthoidichnites* Fitch, 1850

Discussion: Häntzschel (1975) synonymized this ichnogenus with *Gordia*, however, the ichnogenus remains in current usage to describe a levee-lined burrow (Aceñolaza and Tortella 2003; Lucas et al. 2011).

Helminthoidichnites isp.

Figures 5.5C, 5.5D, 5.7
Description: Meandering undermat trails 1.0–1.5 millimeters in diameter preserved as concave/convex hyporeliefs/epireliefs respectively. The trails display a tortuosity generated by a Hofmann's (1990) θ of approximately 17°. The trail may double back on itself to form small loops (Fig. 5.5d, arrow).

Discussion: Levees are not clearly visible on this ichnofossil, therefore it is only provisionally assigned here to *Helminthoidichnites*. *Helminthoidichnites* isp. differs from the Proterozoic ichnospecies *Helminthoidichnites tenuis* by have a less sinuous but more tortuous trail. The latter trace fossil seems to be more directed by intentional, directed motion of the animal (Narbonne and Aitken 1990) rather than a

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more strict adherence to a geometric burrow algorithm as appears to be the case for *Helminthoidichnites* isp.

Material. Field samples, 6-F16-40J series. Six slabs (including two part/counterpart pairs), IGM 4725–4730.

Locality: See geological map, Fig. 5.1.

Stratigraphic position: Unit 2 of the Mina el Mesquite Formation, Sonora, México; age approximately 750–635 million years old.

Ichnogenus *Vaqueroichnus* n. ichnogen.

Diagnosis: Undermat loop trails 1.0–1.5 mm in diameter preserved as concave/convex hyporeliefs/epireliefs respectively. The loops are 3.0–7.5 cm in greatest dimension, and enclose a patch of bedding plane surface where the texture of the biofilm (as a microbially-induced sedimentary structure) is of higher relief or is more rugose than is the biofilm surface outside of the loop trace perimeter. The trackway displays a tortuosity generated by a θ of approximately 2.5°.

Discussion: *Vaqueroichnus* is presumed here to have been formed by the same trace maker that formed *Helminthoidichnites* isp. The two types of tracks have the same burrow diameters, and occur closely associated with one another in a Proterozoic setting where no other ichnofossils appear to be present. One tiny circular loop 8 millimeters in diameter also occurs as part of this ichnogenus and ichnospecies (Fig. 5.6; specimen 6-F16-40J[C′]), and even in this small example the enhanced biofilm texture/relief may be seen inside the 8 millimeter diameter loop. The enhanced biofilm inside of the loops is hypothesized here to represent farming of the biofilm microbes, either for direct consumption by the tracemaker metazoan, for oxygen released by the microbes (“oxygen farm”), or for other substances produced by the presumably photosynthetic microbes.

Etymology: Ichnogenus named for Spanish *vaquero*, “herdsman” or “cowboy,” in recognition of the hypothesized microbe-herding, ‘corral’ aspect of this trace fossil.

Vaqueroichnus stewarti n. ichnogen. n. isp.

Figures 5.5A, 5.5B, 5.6

Diagnosis: As for the ichnogenus.

Discussion: The most similar Proterozoic trace fossil is the “knotted circular burrow” described from Sekwi Brook in the Mackenzie Mountains, western Canada (Narbonne and Aitken 1990). The sharp turns in the Canadian burrow are much less angular than in *Vaqueroichnus stewarti* n. ichnogen. n. isp., hence the assignment of the latter to a different ichnospecies. Also somewhat similar is a circular burrow from the North Carolina Slate Belt referred to *Gordia arcuata* by Gibson (1989). The loop in *Gordia arcuata* is incomplete, however, and unlike *Vaqueroichnus stewarti* n. ichnogen. n. isp. the *Gordia* loop is open ended.

Putative Mesoproterozoic traces called “irregular trails” by Fedonkin et al. (1994) bear some resemblance to both *Helminthoidichnites* isp. and *Vaqueroichnus stewarti* n. ichnogen. n. isp. Although preservation is not ideal, they have a θ value approaching 15°, and some of the trails have double-back loops comparable to those of *Helminthoidichnites* isp. The traces are associated with "small, faint oval impressions" which may be comparable to the loop trails described here.

The tracks that form partially closed loops as shown in Fig. 5.4 represent an unidentified ichnofossil type, with no evidence for enhancement of biofilm growth on the bedding plane surfaces partially enclosed by the open loops.

Etymology: Ichnospecies named for United States Geological Survey geologist John H. "Jack" Stewart.

Material: Field sample 6-F16-40J. Four slabs (including two part/counterpart pairs), IGM 4725–4728.

Systematic Paleontology

Crown group Aculifera Hatchek, 1891
Total group Polyplacophora, De Blainville, 1816
Order unknown
Family unknown

***Clementechiton* n. gen.**

Diagnosis: A small chiton with triangular-ovoid body valves bearing a prominent pair of steeply-sided lateral riblets with granular surfaces representing the ends of clustered mega-aesthete tubules, a broadly beaked posterior margin of the valve that descends steeply from the mucro, a convex anterior upper surface of the valve that slightly overhangs the concave upper posterior surface of the valve, and a posterior valve edge that is slightly jagged or irregular. The valves lack insertion plates or sutural laminae. Where well-preserved, the granular surface resolves at high magnification to polygonal casts representing the flattened ends of mega-aesthete tubes. Mega-aesthete tubes in profile are seen as slightly curving cones 50–150 μ at their distal ends and up to 200 μ in length.

***Clementechiton sonorensis* n. gen. n. sp. M. A. S. McMenamin and D. Fleury**

Figures 14.1–14.5
Holotype: IGM 7461.
Diagnosis. As for genus.
Material: A single disarticulated body valve (belonging to valve series II–VII, possibly valve V).

Discussion: The granularity of lateral riblets is comparable to similar granule impressions, in exactly the same respective position, of the Cambro-Ordovician chiton *Preacanthochiton* sp. (Preacanthochitonidae) from southeastern Missouri (Vendrasco et al. 2004). In both species the granule impressions appear to be casted ends of mega-aesthete tubes. As noted above, close comparisons may be made between the the mega-aesthete tubes of *Clementechiton sonorensis* n. gen. n. sp. and the mega-aesthete tubes of modern chitons artificially casted by epoxy (Fernandez et al. 2006). Note the mega-aesthete tubes in *Clementechiton sonorensis* n. gen. n. sp. preserved on their sides, as seen in Fig. 14.5 and as indicated in Fig. 14.5 with an asterisk. These comparisons provide clear confirmation of, and compelling evidence for, a chiton affinity for *Clementechiton*.

The new genus and species is known from a disarticulated but otherwise well-preserved, thin-walled bilaterally symmetrical intermediate valve or plate that is approximately 4.2 mm wide. The left lateral riblet is better preserved than the one on the right although they are in a bilaterally symmetrical mirror image relationship. The left riblet and its granular surface may be considered to be a case of exceptional preservation, as the mega-aesthete tubes clustered in this region are casted by siliceous cement identical to that cementing the fine sand grains in the sandstone matrix.

The ratio between the length and width of the plate is 0.70. The height of the plate is approximately 1.3 mm. The posterior margin of the valve is broadly beaked and descends steeply from the mucro. A single pair of prominent riblets (homologous to one of the valve lateral area concentric ridges as seen (Kaas and Van Belle 1987) in valve V of *Leptochiton* (*L.*) *torishimensis* and also homologous to one of the "strong, concentric, terraced ribs" of the valve lateral area (Kaas and Van Belle 1987) of *Leptochiton cajetanus* occur on the lateral margins of the plate. Each riblet is approximately 1 mm in length, curving to follow the lateral contour of the edge of the plate (as do the terraced ribs in the modern species noted above) and ending just beyond the sharp escarpment or edge that occurs at the transition from the anterior part of the plate to the posterior part of the plate as shown in Figs. 14.1, 1.42 and 14.3. The intersection between the valve posterior edge and the riblet forms an anchor-shaped impression in the external mold as seen in Figs. 14.1, 14.2 and 14.3.

This posterior edge is slightly jagged and irregular, typical for leptochitons as seen along the posterior edge of valves (Kaas and Van Belle 1987) in *Lepidopleurus cajetanus*. A comparable posterior valve edge irregularity is seen in the Middle Pennsylvanian chiton *Helminthochiton concinnus* from the Francis Creek Shale near Coal City, Illinois (Smith 1960), and thus appears to be an ancient morphological feature among chitons.

Figure 14.3 shows a dorsal view reconstruction of the complete animal, shown here with a postulated eight articulated dorsal plates and a naked girdle. The extent of overlap between plates is conjectural; valve coverage might very well have been more or less than is shown here. Discovery of an articulated specimen of the Pennsylvanian chiton *Acutichiton allynsmithi* demonstrated that the degree of valve overlap was greater than had been depicted in a reconstruction based on disarticulated plates (Hoare and Mapes 1989).

The disarticulated fossil valve (sample 6 of 3/16/95) is preserved as an external mold at the base of a fine sandstone lamina (1.8 mm thick). Its orientation before burial represents a hydrodynamically stable position for a disarticulated valve on the sea floor.

The anterior, convex upper surface of the valve (Figs. 14.3a and b; equivalent to the dorsal median triangle plus the two lateral triangles in other chitons) slightly overhangs the posterior upper surface of the valve. This is very reminiscent of a comparable overhang as seen in body valves of the Pennsylvanian chiton *Helminthochiton concinnus*. Smith (1960) assigned the genus *Helminthochiton* to the Lepidopleuridae. Kaas and Van Belle (1985), however, placed the genus *Helminthochiton* within an extinct subfamily of the Leptochitonidae, the Helminthochitoninae.

The Leptochitonidae are thought to be among the least evolutionarily derived of the chitons. This is largely because the insertion plates and sutural laminae are weak or lacking in many members of this group, and in any case represent features that could easily reappear as cases of convergent evolution (Vinther et al. 2012), as they would help to reinforce the dorsal sclerite shield.

The valve (Figs. 14.4, 14.5 and 14.6) lacks either sutural laminae (apophysis plates) or insertion plates (laminae of insertion). Both sutural laminae and insertion plates are absent in early chiton lineages.

Locality: Field sample 6 of 3/16/95; GPS coordinates of site are N30°24.041′, W111°57.141′ (average of seven measurements), altitude 526 m (average of six measurements). The fossil occurrence is approximately 5 to 10 m below the Clemente oolite, in unit 4 of the Clemente Formation.

Phylum Echinodermata

Class unknown
Order unknown
Family unknown

Sprincrinus n. gen.

Diagnosis: An early crown group echinoderm with subspherical theca (3.5–4.0 cm diameter), consisting of polygonal plates with rugose ornament, with five ambulacra that extend approximately half way down the theca from the oral region. A ring of "ctenoid" plates occupies the thecal summit. These plates bear deep grooves opening to the adoral side of the plate. The ambulacra consist of an unbranched A-ray ambulacrum and a pair of branched, BC and DE lateral ambulacra. The ambulacra have a raised ridge along the margin. The approximate upper third of each ambulacra is marked by a biserial array of deep pores (these do not penetrate to the theca interior), and in the lower two-thirds the biserial array continues but as a biserial array of rounded ridges on either side of the groove that marks the ambulacral midline. The branch point of lateral ambulacra is adjacent to the thecal ambitus. Thecal plates develop abundant oval epispires with marginal rims. Epispires tend to be round-oval in the lower half of the theca, and elongate-oval in the upper half of the theca.

Etymology: Named for James Sprinkle.

Sprincrinus inflatus n. gen. n. sp. M. A. S. McMenamin, M. C. Hussey and L. P. Zapata Figs. 1.4–1.6

Holotype: MCZ 11473-114674 (see Fig. 18, Plate 25 of Sprinkle [1973]).
Diagnosis: As for genus.

Discussion: The attachment site or holdfast for *Sprincrinus inflatus* n. gen. n. sp. is unknown, however, it may have consisted of a suctorial disc or perhaps more likely a holdfast cemented by extensible collagen gluing (bioglue).

Etymology: Named for the inflated aspect of the test.

Age and Stratigraphic Position: Early Cambrian (*Avefallotaspis maria* Zone; Hollingsworth 2005, 2008), lower Poleta Formation.

Locality: Waucoba Springs, Blanco Mountain Quadrangle, eastern California.

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