Frank E. Zachos

Species Concepts in Biology

Historical Development, Theoretical Foundations and Practical Relevance

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To my parents, with love and gratitude

Preface

The species problem has triggered the publication of an almost infinite number of theoretical and practical studies, including quite a number of books. I should, therefore, perhaps briefly justify the publication of yet another one. In a nutshell, I hope to have written the kind of book that I would have liked to read as an extended review on the various aspects of species concepts in biology when I started to seriously and systematically think about species. I read books and review articles, many of them very good, but I felt there was a lack of a comprehensive but accessible text for biologists who are interested not only in the biological dimension of species but also in the bigger picture and the philosophical underpinning of the topic. Then, a couple of years later, I hesitantly decided to write such a book myself. There are books by philosophers (e.g., Ereshefsky 2001; Stamos 2003; Wilkins 2009a, b; Richards 2010) which are primarily theoretical and historical in scope, and there are books by biologists which usually do not cover much philosophy or history (e.g., Kunz 2012). I have read, and benefited from, all of them, and I have tried to combine these different approaches into a single volume. Although I have some formal training in philosophy and the history of science, I am primarily a biologist, and while I have always had a deep interest in the historical and philosophical dimensions of the species problem, my main perspective is that from the viewpoint of evolutionary biology, systematics, and taxonomy. This book, therefore, is aimed primarily at practicing biologists. Consequently, there is a much stronger focus on practical biological issues than in the philosophical monographs by, for example, Richards, Stamos, and Wilkins. Their books are based on a sound biological background, but it is mostly theoretical evolutionary concepts that they draw from, which is only fair, since philosophers are not occupied with actual taxonomy based on a real set of specimens in a drawer in front of them or with quantifying biodiversity in a comparative context to make informed decisions on which area deserves more protection than others. To biologists, the species problem, however, is most real in exactly such cases. Being a biologist myself, it is of course much easier for me to write a book for biologists, but it also makes sense for a different reason. While the species problem is both a philosophical and a biological issue, philosophers do not by default need to care about species. One can work in philosophy (even in the philosophy of science) for a lifetime without ever dealing with biological species and the problems of their definition and delimitation. This, however, does not hold for biologists. Species in biology are inescapable, in both biological theory and practice! That said, while the topic is addressed in an overwhelming number of biological publications and also features prominently in textbooks of systematics or phylogenetics (e.g., Minelli 1993; Wheeler 2012), it is sometimes astonishing how superficially it is treated by some. To give just one example: In a recent German textbook of more than 300 pages on evolutionary biology, species concepts are given a mere one-and-a-half pages, and only the morphological and the biological species concepts are mentioned—the last couple of decades of the debate on one of the most central issues in evolutionary biology have simply been ignored in a textbook on evolution.

Every biologist knows (and usually dreads) the heated debates on species concepts and species delimitation ("one or two species?"). At the risk of sounding condescending, in my experience (and not only mine) it is remarkable on how low a level such discussions are often held (not just philosophically but also biologically!). The complexity of the issue cannot explain this, because biologists, like other scientists, are used to dealing with complex matters. What may be more important is the fact that evolutionary biology, and within it particularly the species issue, is so central and integral to the life sciences that everyone has (or at least feels they should have) an opinion on what makes a species. When asking biologists about, say, physiology or comparative anatomy, one is not unlikely to hear them admit to the fact that they are not very knowledgeable in these disciplines—but one will hardly ever get the same answer with respect to evolutionary theory or the species problem. However, the species problem is not different in this regard from any other complicated topic—unless we actively occupy ourselves with it, we cannot hope to penetrate its complexity. And herein lies the rub—getting anything beyond a merely superficial overview of the available literature on species concepts to many seems like a Sisyphean task. And it is. The last five years or so I have spent reading almost everything on species I could get my hands on, and yet it would be preposterous to claim that I have read more than a fraction of what is available. I do think, however, or at least I hope so, that I have read the most important publications on the topic and perhaps a good deal more than that. And this is where the idea for this book came from. I wanted to write a book that I myself would have liked to read five years ago. This is why this book is not unlike an extended review article. Except for some evaluations and minor thoughts (that others may well have had or even published before me), I do not claim novelty for what I am presenting. A book like this, being on the interface of science and philosophy, runs the risk of being belittled or looked down upon by philosophers ("trivial" or "too simplistic") while at the same being dismissed by biologists as too theoretical and irrelevant to the practice of their science. I have been aware of this during the writing process, but there was nothing I could do but try to do justice to both sides and hope to succeed eventually.

While this book is, I hope, a coherent whole dealing with the three issues of history, theory and practice of species concepts, I have tried to write the different chapters in a way that they can be read independently, in line with its review character. As a consequence, there are probably more repetitions and cross-references than there would be in a book that is explicitly meant to be read only from cover to cover. I hope this will be excused.

A word on manner of discourse in the scientific community may also be due: when it comes to certain topics, the tone of the debate often gets very heated. In fact, the level of spite and contempt for other people's views sometimes borders on insult (or actually crosses that boundary). One need only browse the commentary section in phylogenetic journals where the foundations of systematics and classification are discussed to get an idea of how bad things can get. At times one is reminded of the nasty kind of religious debates where opponents are frequently accused of heresy. The species debate is unfortunately often similar in that regard as it does not only seem to be a scientific and philosophical but also very much an emotional issue. While I feel strongly about the species problem (and by "feel" I mean an enthusiasm for the topic and a deep conviction that it is important), I do hope that I have not let myself get carried away and that I have treated everyone, both those with whom I agree and those with whom I disagree, fairly and with due respect throughout the book.

I would like to express my gratitude toward people who have helped me in various ways in writing this book. Andrea Schlitzberger, Stefanie Dether, and Sabine Schwarz of Springer Publishers have been a great help and a pleasure to work with. My views on this topic have been sharpened by many fruitful discussions with too many colleagues to list them here by name—both researchers with whom I agree and with whom I don't. The latter have probably been even more important in widening my scope. I am grateful for their willingness to share their opinions and insights with me. Finally, I am deeply indebted to my family, particularly Nicole, for constant support and inspiration.

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Frank E. Zachos

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Chapter 1
Introduction to the Species Problem

"Everything should be made as simple as possible, but not simpler".
Albert Einstein

Species concepts, or more generally, the species problem, are among the most debated issues in biology. Answers to the questions of what a species is, in what ways species really exist (if in fact they do) and how species cannot only be defined but also recognized and delimited, belong at least as much, and some of them rather more, to the realm of philosophy than to that of biology, but at the same time they are of utmost relevance to biologists. There may be biologists who think that philosophy is purely theoretical and perhaps even, at times, somewhat aloof, or in short, providing some underpinning for the big picture, but largely irrelevant to their daily work as scientists. That is not quite true, particularly when it comes to the issue of species. Philosophy of science is not just philosophy about science but also *for* science. Whether biologists can or should learn more from philosophers about species than vice versa I don't know, and perhaps that is not an interesting question anyway, but I think it is fair to say that it is more relevant *from a practical point of view* for biologists to get the philosophy right than for philosophers to get the biology right. If philosophers neglect the biology of species, their theoretical treatment of species might become hollow and detached from biological reality, but they are unlikely to suffer any practical consequences because biological species are first and foremost entities of biology. It is biologists who describe species, count them, use them as proxies for different biological phenomena and analyse their phylogenetic relationships. In that regard (and that one only), philosophy of species and biology are a bit like mathematics and engineering—engineers should know their mathematics, or else whatever they want to build won't work. Unlike failures in engineering, which are very obvious, the case with species and biology is, unfortunately, much more difficult: biologists may continue to use flawed or inconsistent notions of species without ever being aware of it, producing spurious results in, for instance, biodiversity assessments or ecological studies. These flawed applications of species notions in turn may then be the basis of equally flawed decisions in "real life"—prioritization of habitats based on species richness or the conservation status of species taxa are just two obvious examples. There is

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probably hardly any other biological concept that is used so differently and inconsistently as that of species, with sometimes disquieting consequences that have largely gone unnoticed by many biologists.

This introduction is supposed to set the stage for the discussions that follow and to introduce some central terms and issues. The species problem is a prime example of the intricate relationships and interdependencies between science and philosophy. Its theoretical dimension is perhaps primarily philosophical, while its practical side is more firmly grounded in biology, but the overall topic clearly affects, and needs to draw from, both disciplines. Since this book primarily addresses biologists and aims at giving them a readable overview of the main points in the debate, doing justice to Einstein's advice quoted above is, particularly when the philosophical aspects of the species problem are presented, more an issue of not being too simplistic rather than being more complex than necessary. Nevertheless, I will start with a bold claim: in biology—although many biologists may be unaware of it—the species problem may not (anymore) be primarily a theoretical issue but rather a problem of biological and particularly taxonomic practice. In other words, it is much more a problem of species delimitation than of species definition. I am sure that many, particularly philosophers of science, will object to that, and I am not claiming that *all* theoretical issues have been solved. What I mean is that the solution presented by Mayden, Wiley and de Queiroz—that there is a hierarchy of species concepts and that something like the Evolutionary Species Concept, the General Lineage Species Concept or the Unified Species Concept acts as an ontological concept of what a species is (an independent population-level lineage in the Tree of Life) and that the other concepts are rather criteria to identify such lineages—, that this solution is *one* way (perhaps not the only possible) to put the theoretical debate at rest or at least consider it preliminarily sufficiently solved to address the practical difficulties. While I subscribe to the views of Mayden, Wiley and de Queiroz in this regard, this book is not intended to act as a justification and/or substantiation of that claim. Rather, I have been aiming at an unbiased overview of the topic, but I also think it appropriate to admit to and disclose my own fallible views for the readers to evaluate. This way it may also be easier to judge where I have not succeeded in being impartial despite my best intentions.

The remainder of this chapter is devoted to a number of issues an awareness of which goes a long way towards avoiding empty debates about the content of the other chapters. This is especially true when it comes to the distinction between the species *category* and the species *taxon* as well as that between species in taxonomy ("T species") and species in evolutionary biology ("E species"). At the very end of this introduction, I will give a short overview of the book.

1.1 What Is the Species Problem?

The species problem is the notoriously difficult task of finding suitable answers to a complex of questions dealing with species and species concepts. A very succinct sensu stricto encapsulation of the species problem is that this term refers to the fact that "there are multiple, inconsistent ways to divide biodiversity into species on the basis of multiple, conflicting species concepts" (Richards 2010, p. 5). In a wider sense, there are more issues or questions involved here. The most important of these questions are: What is a species? Do species exist outside the human minds, i.e. do they have extramental reality, or are they just artificial categories that we make up in our attempts at ordering and classifying natural phenomena? What is the ontological, or metaphysical, status of species—are they classes, natural kinds, individuals, relations, a combination of two or more of these categories, or something else altogether? Do we need more than one species concept, or will a single concept fit all taxonomic groups and evolutionary processes? In other words, is it possible to find a species definition under which all organisms can be grouped into objective and directly comparable entities or units that deserve to be assigned the same name without mixing apples and oranges? Can species (if they exist at all) be non-arbitrarily delimited from one another? And if they can, how?

de Queiroz (2005a) distinguishes three different species problems: (1) the correct definition of the species category (what is a species?); (2) what are the processes responsible for the existence of species? (3) how should species be delimited? The first two problems are conceptual, while the third is methodological. Since the various species concepts address the first of these three species problems and because this book is about species concepts, one main focus will be on the first of these three problems. However, the other two will also be addressed, particularly the delimitation problem (see Chap. 6). When dealing with the issue of inferring species limits, the focus will be on general aspects rather than detailed methodological approaches that have been proposed in the literature. "Cutting up nature at its joints"—a phrase going back to Plato—is the goal of taxonomy, but partitioning a continuous evolutionary process into discrete units is bound to cause serious problems. Shedding light on these problems is the main aim when delimitation issues are discussed in this book.

1.2 Species and Speciation

A few years ago, I attended a conference talk on speciation. The presenter introduced his paper with the statement that he would not talk about species concepts—"I am working on speciation; I don't have to know what a species is". He said it with a twinkle in his eye, and perhaps he was also being a little provocative, but I still think he meant it. And in spite of the fact that oftentimes it is claimed that the relationship between species and speciation is such that the study of one requires an understanding of the other,[1] I think that he was in principle right. Although obviously not static but still evolving, the pattern of species at any one time horizon can be viewed as a pattern of more or less differentiated groups of organisms. This can be recognized without any knowledge of how this pattern came about. We can recognize stars and their planets in the universe without having the slightest idea of how they originated, and I think that in principle the same holds for species. Some species concepts may be defined with a certain mode of speciation in mind, and perhaps this mode of speciation even gave rise to the species concept, but the pattern remains recognizable regardless of the process(es) that have caused it, and it has been explicitly demanded that species concepts be logically distinct from particular mechanisms of speciation (Chandler and Gromko 1989). It should also be kept in mind that often, although processes (including but not limited to speciation processes) are not explicitly mentioned in a short definition, they may be integral to the notion of species according to a certain species concept: “It bears repeating that we cannot do justice to the biological species concept if we focus all of our attention upon the terse verbal formulae that pass for definitions, and thereby neglect the underlying theoretical criteria that really determine what is and what is not a species” (Ghiselin 1997, p. 93). Ghiselin specifically refers to the Biological Species Concept here, but it applies to other species concepts just as well (also in Ghiselin’s view).

Speciation, on the other hand, is by definition the origination of new species, so it seems plausible to argue that one needs to know what a species is to know when speciation has occurred. However, what speciation first and foremost comprises is the divergence of lineages. In the latter perspective speciation researchers can “just” study divergence processes and leave it up to taxonomists to decide where along the line the boundaries should be drawn. This is in line with Ghiselin (1997, p. 98): “We could define ‘speciation’ by explaining how populations split up and become reproductively isolated, and only after having done so say that the products of speciation are called ‘species’”.[2]

If speciation is viewed as lineage divergence, statements like “speciation in the presence of gene flow” which at first glance might seem paradoxical make perfect sense—the sundering agents leading to divergence outweigh cohesion through gene flow. When speciation is considered a continuous process through time, the exact point at which it is considered to be complete (two species) is not key to an understanding of the whole process anymore. It will be argued in this book that species delimitation in practice is the imposing of a binary taxonomic concept

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[1] Stamos (2003, p. 5), for example, says that “it is generally admitted that any speciation analysis presupposes a species concept”.

[2] Ghiselin suggests this when he explains that one can define species by means of speciation (as its result) which of course means that one then has to define speciation without reference to species to avoid circularity. Ghiselin, being a proponent of the Biological Species Concept, emphasizes reproductive isolation, but the argument is independent of the particular species concept one adheres to.

(species or no species[3]) on a continuous process and a continuous organismic world with vague or fuzzy boundaries. There is therefore a grey area in all but the most clear-cut cases of divergence between sister lineages. This means (at least in my view) that, while species and speciation are of course not decoupled from each other, their mutual dependence when it comes to understanding them tends to be exaggerated.

1.3 Species Homonymy: One Word, Multiple Meanings

The term species is used with quite different meanings in different contexts which often causes unnecessary confusion. Hey et al. (2003) distinguish three different predominant meanings—(1) the species category, (2) the word applied to a particular taxon with the rank of species (their example is the species taxon *Homo sapiens*) and (3) the word applied to a particular "evolving group of organisms" (p. 599). The first, the species category, is the class of all species taxa. This pair of terms will be explained in the following section. The species taxon, i.e. a particular lineage in the Tree of Life that is assigned species status, is the species of both latter meanings given by Hey et al. (2003), i.e. (2) and (3). These two aspects of the species taxon, the taxonomic and the evolutionary, will be addressed in the section after the following. Reydon (2005) also thinks that the term species is used homonymically and that it denotes four distinct scientific concepts. His view will briefly be summarized in Sect. 3.6.

1.3.1 The Species Category and the Species Taxon

It seems obvious that the term species has two very different meanings, but nonetheless these two are often conflated. The *species category* is the hierarchical level or rank in the Tree of Life that we call species. The *species taxon* is a concrete lineage in the Tree of Life at the species level, e.g. *Homo sapiens* or the tiger (*Panthera tigris*). The species category is the class of all species taxa, and a species concept defines the species category, i.e. it tells us "what species taxa have in common so that they are members of the species category" (Ereshefsky 2001, p. 80). This definition then applies to all species taxa or at least those species taxa within the group to which the species concept is applied if it is not universal. This ambiguity is by no means particular to the term species but is the rule rather than the exception. "Chair" is also an abstract class and a concrete object at the same time.

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[3] This holds regardless of the availability of intraspecific categories such as subspecies or evolutionarily significant units; rather, it applies to these categories just as much as it does to the species category.

Chair as an abstract class is a device with legs to sit on, whereas the chair that I am sitting on while writing these lines is a concrete instance of the class of chairs. In the same way, every species *taxon* (humans, tigers, etc.) is an instance of the class of species, i.e. the species *category*. Similarly, parents as a class are all humans that have children, while two instances of that class are my parents Rose and Bill, and so on. Only classes have instances and defining properties, while concrete objects or individuals do not. Consequently, a definition in the usual sense of the word can only be given for the species category (in the form of a species concept). Concrete objects or individuals and species taxa (if they are individuals in the philosophical sense), on the other hand, cannot be defined by naming some property, but only by pointing them out, which is called an ostensive definition, and is similar to the act of christening (Ghiselin 1997, p. 46). *Homo sapiens* or tiger, just like Rose and Bill and the chair I am sitting on, cannot be defined by means of necessary and sufficient properties, but the species category, parents and chair in the general sense can—by a species concept, having children and being a device for sitting with legs, respectively. These issues will be dealt with in more detail in Chap. 3 when the ontology of species is discussed, in particular, whether species taxa are classes of organisms or individuals. An awareness of the difference between the species category and the species taxon is also key when it comes to the question whether species really exist (in an extramental sense, i.e. outside the human mind), because the answer to this question can be different for the category and the taxa that we call species. More will be said on this when the ontological positions referred to as species nominalism and species realism are dealt with (see Sect. 1.5).

1.3.2 Taxonomic Species vs Evolutionary Species

Another very important distinction is that between taxonomic and evolutionary species or T species and E species[4] (e.g. Endler 1989; Williams 1992; Ghiselin 2001). Both refer to species taxa, not the species category. T species are the species as named by taxonomists, while E species are the species that partake in evolutionary processes or are units of evolution. T species denote taxa, and E species denote objective entities. Ideally, the two are identical, i.e. taxonomists correctly identify and delimit natural units at what we believe is the species level in our systematization of the living world. More realistically, T species are an approximation of E species, but since taxonomy is discrete while evolution is continuous (sharp vs vague boundaries) and because there is hardly ever enough knowledge on what is being named a T species to really equate it with an E species, we cannot necessarily expect T species to always (or even very often) capture E species in a precise manner. This becomes particularly obvious when looking at numerical taxonomy

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[4] Evolutionary or E species in this context must not be confused with species according to the Evolutionary Species Concept! The term E species has a much more general meaning.

whose adherents explicitly warn against mixing up phenetic species with evolutionary units (Sokal and Crovello 1970[5]), but it applies to all taxonomic schools. Only under rare and ideal conditions is a T species obviously also an E species: a single endemic geographically limited and genetically homogeneous population. T species are much easier to erect than E species: a single fossil fragment or even a highly divergent DNA sequence may be enough to (at least preliminarily) describe a new T species, but it is obvious that after this we still know almost nothing about the underlying evolutionary entity that the new name is ultimately attached to. We do not know about the majority of that entity's characters and its extension (which organisms belong to it and which don't), let alone its ecology and behaviour. In fact, we do not even know whether there is such an entity (because new data might show it to be the same as an already known species after all). Under species pluralism (see below), there may also be very different and non-overlapping kinds of E species (e.g. reproductively isolated species vs ecological species vs monophyletic species, etc.). Because there are rules according to the different nomenclatural codes (zoology, botany, microbiology) that require a binomial for described species, organisms that are quite different with respect to their roles as evolutionary entities will receive the same kind of species name (genus plus species name). This is most obvious when it comes to sexual vs asexual organisms. There is a considerable body of literature dealing with the question of whether sexual and asexual organisms both form species or, more exactly, whether what we call species in one is actually really the same as or directly comparable to what we call species in the other (see Sect. 5.1). Many authors deny the existence of asexual species because they lack reproductive cohesion (which is often viewed as a necessary property of species). If this is true, then there are no asexual E species, but asexuals are nonetheless given binomial species names and thus exist in our classifications as T species: "The real justification for this claim [that species concepts should include all organisms] is the supposed advantages that we would have from being able to refer to each and every organism by a specific epithet, and to do so in what seems, at least, to be a straightforward manner. We lose, however, the advantage of having the most basic unit in systematics coincide with one of the most basic units in theories of evolutionary processes" (Ghiselin 1997, p. 103).

Very often, T species are taken at face value, i.e. treated as if they were E species as well. This, however, is an oversimplification of the natural world. T species should really be seen as hypotheses of E species (see also Baum 1998; Hey et al. 2003)—hypotheses that in some cases have better or more evidence in their favour than in others. Except when studying well-known species, a default attitude of scepticism as to the identity of T species and underlying E species seems advisable.

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[5] "… the phenetic species as normally described and whose definition may be improved by numerical taxonomy is the appropriate concept to be associated with the taxonomic category 'species,' while the local population may be the most useful unit for evolutionary study" (Sokal and Crovello 1970, p. 149).

Finally, apart from being taxonomic and evolutionary units, species are also the most fundamental currency in biodiversity. Biodiversity species ("B species"), however, are not as distinct as T or E species. In point of fact, in most cases they are simply a means to an end: a proxy to quantify biodiversity and compare diversity values among different groups and/or regions. Most biologists would probably agree that ideally these "B species" should be true E species, but in practice species counts will have to be based on T species. Because of the shortcomings of T species (and subspecies), alternative concepts have been introduced in conservation biology and biodiversity research (such as phylogenetic diversity and Evolutionarily Significant Units or ESUs, see Sects. 5.9 and 7.2), and it has even been insinuated that we might actually need two different classifications: one for practical needs (T species regardless of their evolutionary status) and one listing only objectively delimited evolutionary units (see Sect. 6.1). Whether this is feasible or even theoretically possible is doubtful.

1.4 Synchronic (Horizontal) Species vs Diachronic (Vertical) Species

Species can be viewed in a single slice of time (e.g. the present), comprising contemporaneous organisms, or they can be viewed as entities existing through time. The first is the synchronic dimension and the latter the diachronic dimension—or time-limited and time-extended dimensions, respectively (Baum and Shaw 1995; Baum 1998). To many, it seems very obvious that the two are really just two sides of the same coin and that the diachronic species is made up of an infinite number of synchronic time slices in which the species exists. Synchronic species, as Baum and Shaw (1995, p. 300) emphasize, are "analogous to the instantaneous morphologies (semaphoronts) that make up the development pathway of organisms" (Hennig 1966). That is, the synchronic species is a "snapshot" viewpoint as opposed to the historical viewpoint through time (Endler 1989, p. 627).[6] I would argue that one (synchronic) is just a simplified version of the other (diachronic), but Stamos (2003, p. 79 and throughout his book) thinks that the synchronic dimension of species is ontologically superior to the vertical one: "it seems to me that horizontal species are logically and therefore ontologically prior to vertical species. My reasoning is simple. The reality of vertical species necessarily entails the reality of horizontal species. But the converse is not also the case" (p. 79; see also Stamos 2002). To be fair, he does not deny that species have a vertical reality; only that their horizontal reality does not depend on the vertical reality. And when he talks of the temporal

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[6] Endler (1989) also distinguishes between taxonomic and evolutionary species (T species and E species, see Sect. 1.3.2). The snapshot or synchronic view of species vs the historical or diachronic view he calls contemporaneous and clade species concepts. He considers these two groups (contemporaneous and clade concepts) as the two main subgroups of the E species with the contemporaneous concepts particularly popular in evolutionary biology and the clade concepts in phylogenetic systematics, "with palaeontology falling somewhere in between" (p. 627).

dimension, he thinks in geological terms and time scales, not about a certain species, say *Homo sapiens*, today vs the same species yesterday. But ontological priority or superiority entails a difference in ontology nonetheless, even it is a difference in degree, not in kind, and how would such a difference be justifiable? Quite apart from the fact that there is no principal difference between two time slices one day apart and two such slices separated by millions of years, this emphasis of an ontological difference between the synchronic and diachronic dimensions seems to me artificially inflated: if species are spatiotemporally extended individuals, then there is just a single individual through time. On this view, there cannot be an *ontological* difference between synchronic and diachronic species (or superiority of one over the other) as these are really just two sides of the same coin. Am I as a person more or differently real in an ontological sense today and yesterday and tomorrow separately, i.e. at any single time slice, than through my whole life combined!? I don't think so: "An individual may be viewed from a **synchronic aspect** (a slice in time) or a **diachronic aspect** (through time), but its ontological status is thereby unaffected" (Ghiselin 1997, p. 307, bold in the original). And Ghiselin again: "Individuals need to be envisioned in the context of the temporal dimension, in other words diachronically rather than just synchronically, and not as if they were different things at different times" (Ghiselin 1997, p. 48). Thus, the fact that "[t]here is an amazing recalcitrance in many theorists to admit this distinction" (the one between the horizontal and the vertical dimension of species, Stamos 2003, p. 316) may well be due to there being no such fundamental (i.e. ontological) distinction in the first place. Stamos is an accomplished philosopher of science, and I am hesitant to say this, but it seems to me that he mixes up ontological with operational priority. Epistemiologically or operationally (i.e. in taxonomic practice), synchronic species are easier to handle, and it may be argued that this is almost always the case if the synchronic time slice is the present because any two lineages will have been separated from each other longer today than at any point of time in the past, so that divergence is maximized by comparing two species today and not at an earlier stage of lineage sundering. This divergence will further increase in the future so that future "present" time slices will have even more priority on this view. Hey (2001a, p. 151) agrees with the view that the difference between synchronic and diachronic species is artificial and that it is emphasized to avoid problems in biological practice: "any suggestion that both views of reality, contemporaneous and historical, can be sustained as distinct and valid must suppose two different sorts of reality. The motive for treating historical and contemporaneous views distinctly is of course, that as soon as one envisions them as the same, one must embrace all of the difficulties of indistinct boundaries and fractal hierarchies that are well known as part and parcel of the evolutionary process". Also, extant species are much easier to study and there will always be more data available (including direct observation of the living organism) to base taxonomic decisions on. Exceptions to this rule only occur if we are at present witnessing the merging of two or more not yet irreversibly diverged lineages as seems to be the case with some cichlids, where declining water transparency due to eutrophication leads to the breakdown of colour-based mate-choice-mediated isolation of still interfertile lineages (Seehausen et al. 1997; Maan et al. 2010; for similar examples in other fish species and Darwin's finches, see

Seehausen 2006, Vonlathen et al. 2012, Grant and Grant 2014, Kleindorfer et al. 2014 and references therein). In this case, however, it might be argued that there never was more than a single species in the first place but rather that the lineages are/were species in statu nascendi. This is yet again another example of nature being messy and having fuzzy boundaries.

Walter Bock takes an even more extreme position when it comes to the synchronic and diachronic dimensions of species. He only recognizes species as synchronic entities, the diachronic dimension he calls phyletic lineages. A species is "the complex of interbreeding individual organisms co-existing at one point in time which is genetically isolated from other such complexes", whereas a phyletic lineage is "the time-line of the species resulting from it reproducing itself generation after generation" (Bock 2004, p. 179). Two horizontal, i.e. synchronic, time slices as cross sections through the same phyletic lineage at different times are neither the same nor different species according to Bock (see Fig. 1 in Bock 2004); in fact on his view "[i]t is a non-question to ask whether these different time slices of a phyletic lineage represent the same species or different species [. . .] it is not possible to speak of the origin or the birth of a species, nor is it possible to speak of the age of a species. All existing species are of equal age, or in other terms, all species are ageless. Species boundaries are real only in horizontal comparisons, which are between different lineages (Bock 1989), and do not exist in vertical comparisons (within a single phyletic lineage)" (Bock 2004, p. 179). The distinction between species (horizontal) and phyletic lineages (vertical) may seem as a merely terminological issue (by denying to call the vertical dimension species and simply giving it another name), but it actually goes deeper than that: Bock argues for a completely non-dimensional species concept in time. However, either the difference is artificial and the phyletic lineage is nothing but the sum of the species at infinitesimally small time slices or the same mistake with respect to a difference in ontology of species in time vs species or lineages through time is made as pointed out above. The fact that Bock considers the question if two time slices of the same lineage refer to the same or different species as logically inadmissible suggests the latter of these two possibilities. Bock is an adherent of the Biological Species Concept, whose defining property, interbreeding or reproductive/genetic isolation, cannot be applied through time, which may also explain his views. In any case, it seems that taxonomy on the whole, on Bock's view, cannot deal with species but only with phyletic lineages because if it is a "non-question" whether a tiger 200 years ago and one today are the same species, they cannot have the same species name either but only belong to the same phyletic lineage.

Viewing the synchronic and diachronic dimensions of species as ontologically equivalent might also contribute to the solution (or rather dissolution) of the alleged difference between species as dynamic units within processes vs the results of such processes. Dobzhansky (1937, p. 312) has famously stated that "Species is a stage in a process, not a static unit",[7] whereas Mayr (1942, p. 119) insists that species are

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[7] See also the title of one of his other publications: "Speciation as a stage in evolutionary divergence" (Dobzhansky 1940). This is also in accordance with de Queiroz (1998, p. 70f.)

the results of a process. Viewing species synchronically, they appear as the (preliminary or in the case of extinct species: final) result of the process of speciation or more generally: divergence. When taking the whole lineage of the species through time into consideration and admitting that there is a grey area as to when two diverging lineages cross the threshold of speciation and are thus to be regarded as two separate species, the synchronic snapshot view appears more as the stage in a continuous process. And of course non-extinct species can split into daughter species in the future, which means that whatever result they are today, they can always be viewed as a stage in a process from a future perspective. Ghiselin (1997, p. 94) thinks that Dobzhansky's statement implies a category mistake ("like defining 'undergraduate' as a stage in education, rather than as someone in that stage"), and that may, strictly speaking, be correct, but I think that Dobzhansky mainly aimed at pointing out that species are part of a continuous process and that boundaries are therefore necessarily fuzzy. The stark distinction between these two perspectives therefore seems partly artificial or at least inflated.

One might wonder if the synchronic/diachronic dichotomy is not just a purely philosophical exercise about what it means to be the same through time (such as the classical paradox of Theseus' ship[8]), but in fact these two aspects of being a species come up in many discussions. For example, the Biological Species Concept has been called non-dimensional precisely because it is only applicable in synchrony (and, strictly speaking, also in sympatry), and it has been claimed that the only meaningful way to speak about species is in their synchronic or time-limited dimension. Many, however, myself included, would object to that view.

1.5 Important Species "–isms": Realism vs Nominalism and Monism vs Pluralism

Realism and nominalism are philosophical terms with a long history that is not relevant in detail for our purposes. The Cambridge Dictionary of Philosophy (Audi 2009, p. 562) defines (metaphysical) realism as "in the widest sense, the view that (a) there are real objects [. . .], (b) they exist independently of our existence or our knowledge of them, and (c) they have properties and enter into relations independently of the concepts with which we understand them or of the language with which we describe them", while nominalism denies the existence of these objects

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who, within his General Lineage Species Concept, views many traditional species concepts as criteria not for the status as species but for different stages in the existence of species (see Sect. 5.2).

[8] This ship is constantly under repair so that eventually every single of its original planks has been replaced by a new one. The question now is whether the ship is still numerically the same or not. And what if the old planks had been repaired later and used to build a new ship? Would that new ship then be the 'real' ship of Theseus? This paradox about what makes sameness has been discussed by philosophers from Greek antiquity through to the modern era.

independently of the human mind.[9] The terms are usually used in the context of the so-called problem of universals. One main issue of medieval scholastic philosophy was the question if universal terms (such as white in general as opposed to a particular white object, or the concept of chair as opposed to a particular chair like the one I am sitting on right now) are real or not. As in the definition of realism above, by real is usually meant the idea that a real unit or object has extramental reality, i.e. does not only exist in our minds. Realism grants such reality to universals, while nominalism does not. In the context of species, the question of course then is whether species have extramental reality or not. Put the other way around: do species only exist in our minds, or are they real natural entities independent of our reasoning? Particularly with respect to the views of Charles Darwin, there has been a long debate about this question (see Sect. 2.3). The first thing one has to realize, however, before an answer can be given is that this question really comprises two questions: one regarding the species category and one regarding the species taxon. Confounding these two concepts has caused great confusion in discussions about the reality of species. One can be a species realist with regard to species taxa, while at the same time denying reality to the species category. In this case one would accept that species taxa such as *Homo sapiens*, tigers or ginkgo trees exist in an objective way in nature, but that they are not directly comparable entities, i.e. that what we call the species category lumps incommensurable individual taxa into an artificial category that we, knowingly or unknowingly, only use for convenience's sake. On the other hand, one can hold that not only species taxa but also the species category is real in the extramental sense. In this case all species taxa would indeed share common and comparable qualities that justify their being assigned the categorical rank of species in taxonomy (= species category).[10] If species taxa are individuals (see Chap. 3), their reality is automatically implied, and since most biologists today (and at least many philosophers) subscribe to the individuality thesis, the reality of species taxa is usually agreed upon. It is perhaps interesting to note that species taxon realism was sometimes viewed as incompatible with evolution. As long as species were regarded as the result of divine creation, their reality was obvious, but as soon as it became clear that species changed and evolved into new species, species taxon nominalism would not seem unreasonable anymore because then boundaries were suddenly vague and species became "slippery" entities. Wilkins (2009b, p. 119f.) lists the botanist Charles Bessey, a student of Asa Gray's, as an example for a biologist who denied the reality of species for this very reason. This view, however, is rare today, and the fact that boundaries are fuzzy is not seen as an argument against the reality of species taxa anymore.

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[9] Things are not as simple as this dichotomy might suggest, of course. In Sect. 3.1 I will briefly mention that a trichotomy (realism, conceptualism and nominalism) may be more correct.

[10] Wilkins (2009a, p. 221) bemoans that Mayr and others have called species nominalism the opposite view to species taxon realism (this nominalism is then species taxon nominalism) because in philosophy, from which the term is taken, nominalism typically is assigned to a view denying universal reality, and therefore the logical usage would be for species category nominalism. Wilkins suggests species deniers for those who think that species taxa are not real.

Whether there is really an objective level of the species *category*, i.e. an objective species rank in the hierarchy of the Tree of Life, is a different matter, though. There are authors who deny this, and their arguments are not easily dismissed (see Sects. 3.6 and 7.2). What complicates matters further is the possibility that, even if there is an objective species level in taxonomy, there may be more than one, i.e. there might be not only one kind of species category but two or more. For example, organisms may be meaningfully combined into species of one kind, e.g. reproductively isolated biological species, but also—just as meaningfully—into species taxa of another kind that do not completely overlap with the first—e.g. differently adapted ecological species and/or species according to a multitude of other concepts listed in Chap. 4. If all these classifications are equally justified, perhaps no single species concept has primacy over the others? This is the position of species pluralism, whereas species monists argue that there is a single best species concept. There are variations on this theme, e.g. ontological vs operational species pluralism—the former holding that there really are different kinds of species, while the latter only accepts a single type of ontological species category but argues that there are many different criteria by which this category can be identified. A brief discussion of these questions will be given in Sects. 3.6 and 5.2. Somehow related is the contentious issue dealt with in Sect. 5.1, namely, whether some organisms, in particular, asexuals, do not form species at all, as claimed by many adherents of the Biological and the Hennigian Species Concepts.

1.6 General Remarks on Terminology and Recurrent Arguments

One recurrent issue or argument throughout the book is the existence of fuzzy or vague boundaries when it comes to species in biology. Nature is messy, and this is a central topic of the species problem and many biological phenomena that are of relevance to it. Among the latter is, for example, reproduction: biologists tend to contrast sexually and asexually reproducing organisms, but in reality this is a spectrum with obligatorily sexual reproduction on the one end and exclusively asexual reproduction (as in the famous bdelloid rotifers) on the other—with all kinds of shadings in between where organisms switch between the two or are at least capable of both. Interbreeding and gene flow are also somewhat messy terms—how often must mating be successful for two organisms or taxa to count as capable of interbreeding? How often must genes be exchanged between two gene pools for the latter to be called a single gene pool? How ecologically different must two populations be to be classified as inhabiting different ecological niches? From this short and arbitrary list, it becomes obvious that many of the short and terse definitions used in species concepts (see the list in Chap. 4) make use of terms that are not as unambiguous as they may seem at first glance. It becomes even more difficult when it comes to species limits themselves, but this fuzziness is not a shortcoming of evolutionary theory, biology in general or philosophy, but it is inherent in nature and a direct consequence of the process of evolution which ultimately is nothing but the minute changes occurring during reproduction in every generation accumulated through time. At low taxonomic levels, we should expect grey areas of divergence; if there were none, evolution would be basically refuted. In a nutshell, one of the main reasons for the species problem could be phrased like this: *taxonomy is a discrete ordering system imposed upon the continuous structure of the Tree of Life*. Taxonomy therefore inherently oversimplifies the natural world, and ultimately we will probably have to live with the insight that in many cases the continuous process of evolution cannot be adequately captured by a basically binary approach (species or no species). Hey (2001a, b, p. 47) puts it more generally and goes beyond our taxonomic efforts to locate the root of the problem when he says that the basic problem is that language is discrete, while much of nature is continuous. He even imputes to us “a predisposition to misunderstand species” (ibidem, p. 66). His view on why this might be so will be briefly summarized in Sect. 3.4. Fuzzy boundaries, however, do not preclude the identification of species; rather they are a very widespread phenomenon. For example, clouds and diseases are not easily delimited, and yet we have a clear concept of them and readily identify them in most cases. Wilkins (2011, p. 60) is in accordance with this view when he says: “neither is it the case that species are unreal because they shade into each other. In modern philosophy, there is an ongoing debate over whether one can have vague and fuzzy sets or kinds, but for science we need only a little logic and metaphysics: If we can identify mountains, rivers and organisms, we can identify species”. In this regard, incidentally, species seem comparable to pornography about which Potter Stewart, former Associate Justice of the Supreme Court of the United States, famously said that he might not be able to define it but “I know it when I see it”. In many cases this famous quote is just as applicable to species as it is to obscenity.

This said, I should perhaps also add a word on the use of extreme examples or scenarios to uncover weaknesses in species concepts. In many critiques of certain species concepts (usually combined with praising the author’s own favourite), extreme cases are pointed out that make the concept under scrutiny seem bizarre and are supposed to serve as a kind of reductio ad absurdum. For example, the Cladistic Species Concept that defines species as the lineage between two cladogenetic splits (= speciation events) is often criticized for completely disregarding anagenetic change so that animals as small as a mouse that evolve into behemoths the size of an elephant along one unbranched lineage must still be considered the same species. However, it should be made very clear from the beginning that *all* species concepts have odd consequences in extreme cases and that they all are a compromise and a trade-off between pragmatic requirements and theoretical consistency. I have yet to see a species concept that does not suffer from this.

An issue that will not be dealt with in depth in this book is the analogy of species and languages. Comparing the two seems obvious and natural, and much has been written about the similarities of biological and linguistic evolution and the use and application of phylogenetic methodology to linguistics (see, e.g. Ghiselin 1997, pp. 138–144; Stamos 2002, 2003, 2007; Mendívil-Giró 2006; Pagel et al. 2013 and references therein). A linguistic analogue of phylogenetics is older than phylogenetics in the biological sense, and the influence of the linguist August Schleicher on Ernst Haeckel at the University of Jena in Germany is well known. Schleicher already pointed out the analogy between the difficulties of separating languages from dialects on the one hand and species and varieties as mentioned by Darwin on the other (see Ghiselin 1997, p. 139). It is this delimitation analogy (not the one regarding evolution and phylogenetic relationships in general) between languages and species that I will take up in Sect. 6.3.

Finally, a few words on terminology. A term that is often found when it comes to systematics and evolutionary biology is typology. The term obviously relates to "type" but there are quite different meanings of type: types in nomenclature (as in holotype or paratype), archetypes as idealized concepts in morphology and others (see Farber 1976). Also, typology is often used synonymously with essentialism (e.g. by Mayr and Ghiselin), while other authors hold that the two are quite different: according to Wilkins (2009a, p. 91), types (but not essences) can be instantiated in degrees, and there can be variation from the type (but not from the essence). Particularly through Ernst Mayr's influence, the term often became viewed as the pre-Darwinian Platonic antithesis to modern evolutionary "population thinking". Given the term's ambiguity, however, I will refrain from using it wherever possible.

Another term, one that I am using very often and that indeed features in the title of this book, is concept. I will not go into the details of the naming and misnaming of notions as concepts in the context of the species problem. Wilkins (2011) distinguishes concepts and conceptions and holds that there is basically a single species concept but ca. 30 species *conceptions*. That may well be true. However, since all these conceptions have been called "concepts" for decades (one rarely comes across the biological, ecological or phylogenetic species "conception" in the literature), I stick to that tradition and will only briefly address this issue at the beginning of Chap. 4. What I will highlight, though, is the fact that not all species concepts are the same kind of concepts, but that some are true ontological concepts (about what a species is), while the majority are rather operational criteria that give guidelines of how to identify species.

1.7 Overview of the Remaining Chapters

After this short introduction, two chapters deal with the historical development of species concepts (Chap. 2) and the ontological or metaphysical status of species (Chap. 3). Both of these are only short summarizing overviews. Any claim that these overviews even come close to something bordering on near completeness would be preposterous. An exhaustive treatment of these topics, however, is not necessary. In line with the general aim of this book, a summary of the main arguments is sufficient. In fact, I wasn't even sure whether I should include the historical chapter as it might be argued that, while certainly interesting, the development of notions of species through time does not add to a deeper understanding of the present debates. I don't think that this is entirely true, though. Rather, an awareness of the history of species concepts does shed at least some light on issues that we are still struggling with, particularly when it comes to the (mis) conception that pre-evolutionary notions of species were largely governed by some version of Platonic or Aristotelian essentialism. Still, Chapters 2 and 3 should be best viewed as extended abstracts of the topics they are dealing with. Interested readers are kindly asked to turn to the more technical and detailed publications that I make reference to in those two chapters.

Chapter 4 contains an annotated list of 32 species concepts. Any such list necessarily contains some element of arbitrariness, but I give some justification and explanation which concepts I have included and why.

Chapter 5 highlights some issues related to various species concepts. Some of these concepts, such as the Biological Species Concept and versions of the Phylogenetic Species Concept, will be explicated more detailedly than in Chap. 4, but more general issues such as the question of whether asexual taxa form species and whether ancestral (stem) species necessarily become extinct upon speciation are also discussed. The purported (theoretical) solution to the species problem as suggested by Mayden, Wiley and de Queiroz—that there are two different kinds of species concepts, ontological and operational ones—is also presented in some detail, as is the issue of microbial species and intraspecific categories (such as subspecies and ESUs).

Chapter 6 deals with species delimitation. This is the major rub when it comes to biological practice, of course. While I mention some methodological approaches to dealing with the delimitation problem, I focus on the underlying issues here, arguing that completely non-arbitrary delimitation guidelines are illusory and that this is not a consequence of our limited knowledge or intellectual powers but rather a logical consequence of evolutionary patterns and thus nature itself.

Chapter 7 is devoted to perhaps the most disquieting corollaries of the species problem, namely the consequences that the application of different species concepts has on ecological and evolutionary studies, and—even more unsettling—that many of these studies may be inherently impossible or flawed if there is no such thing as a single objective species concept that fits all taxa.

Finally, Chap. 8 briefly summarizes the content of this book, providing something like a short list of "take-home messages".

Chapter 2
A Brief History of Species Concepts and the Species Problem

As stated in the title of this chapter, this is only a very short overview. It aims at giving a readable historical summary for biologists and, more particularly, at pointing out a number of misconceptions about the historical development of the notions about species in biology. A more detailed account can be found in the first chapters of Richards (2010) and in Wilkins (2009a, b). The two books by Wilkins are the most extensive ones on this topic and highly recommended to anyone with a deeper historical interest. One is a monograph and the other is an annotated sourcebook, a highly useful collection of quotations and passages from the most important original publications through time with a short introduction to each period. I have learned a lot and drawn extensively from these three books. This includes not only the passages quoted from them but also many passages from original sources that I found in these books.

This chapter will be subdivided into four sections: (1) an introduction to the historical misconception that has been named the Essentialism Story or the Received View, (2) a summary of notions about species from Greek antiquity (i.e. Plato and Aristotle) until immediately before Darwin, (3) a short overview of Darwin's (alleged) views and (4) the last part that covers the post-Darwinian time, i.e. the evolutionary age, up to the Modern Synthesis in the mid-twentieth century. This subdivision is a very traditional one and in fact owes much to the misconceptions depicted in the first section, namely, to juxtapose pre- and post-Darwinian views on species as the two big counterparts. This is due largely to a misrepresentation and oversimplification of the views on species up to the nineteenth century. Rather than dividing the history of species concepts temporally—e.g. as is often done, before and after Darwin or before and after the acceptance of evolution—Wilkins (2009a, p. 9) has made the good point to distinguish two traditions of thought when it comes to the species problem: universal taxonomy and philosophical logic on the one hand and explicitly biological conceptions of species on the other. This is important because the term "species" (as well as that of "genus") and its definition and demarcation have a long philosophical history independent of the science of biology or even biological questions. They play an important role in

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Aristotelian and thus also in medieval logic (when Aristotle was the authority on everything philosophical), and it was this tradition of a universal (not restricted to biology) taxonomy from which was derived what we today know in biology as the taxonomic categories species and genus. The universal debate has thus paved the ground (through, among others, Abelard, Roscelin and Ockham) for these categories to be included into "the nascent biological sciences in the seventeenth century" (Wilkins 2009a, p. 36). For the sake of an at least primarily chronological overview, however, I have kept the traditional structure. This structure suggests Darwin as the central turning point, but it will become clear that in many important ways with respect to the history of species concepts, he was far less revolutionary than often claimed, and that is not so much due to what Darwin said or thought but mainly due to the fact that pre-Darwinian thinkers were much less dogmatic and essentialist than the traditional view of the history of biology has it.

2.1 The Essentialism Story

The traditional view on the historical development of species concepts among historians of biology has been challenged and perhaps even fundamentally changed over the last 10–15 years. This traditional view—named Essentialism Story or Received View and now by many believed to seriously distort the historical facts—has it that Platonic idealism with its transcendental ideas and eternal essences was the prevailing ontological underpinning for more than 2000 years when it came to biological species, doing a lot of damage to scientific progress and particularly impeding anything akin to evolutionary thinking. Essentialism refers to the concept that there are certain necessary and sufficient properties to an entity that make it what it is. The most cited textbook example is the definition of a bachelor as an unmarried man, i.e. for someone to be a bachelor he has to be a man and must be unmarried. These two properties are both necessary and sufficient—all bachelors are unmarried men, and to be an unmarried man means to be a bachelor.[1] For species this means that all individuals of a species have at least one such necessary and sufficient property in common that makes them members of that species, and that every individual showing this or these properties is automatically a member of

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[1] Because essential properties are only those which are defining or explanatory (make an entity what it is), they cannot be accidental or contingent. If by chance all bachelors and only bachelors wore red shirts, wearing a red shirt would not be an essential property of bachelors because it would not capture the "essence" of what a bachelor is, but red shirts would still be suitable to identify bachelors (although not to define them). Classification based on unequivocal properties (present in all and only members of a certain entity) that are, however, accidental is sometimes called nominal essentialism. While Aristotle believed it was possible (although often difficult) to find true essences, Locke was more sceptical and thought that real underlying essences were present but hidden from us. Instead, he focused on operational essences to identify entities unambiguously; his essentialism was therefore primarily nominal (see, e.g. Ereshefsky 2001, p. 22).

that species. The view on essentialism in biology according to the Essentialism Story is nicely summed up in the title of an early paper by the philosopher of science David Hull: “The effect of essentialism on taxonomy: Two thousand years of stasis” (Hull 1965). Essentialist thinking was then, so the story goes, eventually overcome by Darwin whose evolutionary revolution replaced essentialism with what Ernst Mayr has famously called population thinking: “The ultimate conclusions of the population thinker and of the typologist are precisely the opposite. For the typologist, the type (eidos) is real and the variation is an illusion, while for the populationist the type (average) is an abstraction and only the variation is real. No two ways of looking at nature could be more different” (Mayr 1959, p. 2, quoted from Ghiselin 1997, p. 77).[2] This view—that there is a clear dichotomy between pre-Darwinian Platonic (and/or Aristotelian) essentialism on the one hand and Darwinian and post-Darwinian evolutionary population thinking on the other—has been widespread among both philosophers[3] and biologists. An example from philosophy is Daniel Dennett who claims that “[t]he taxonomy of living things that Darwin inherited was thus a direct descendant, via Aristotle, of Plato’s essences” (Dennett 1995, p. 36, quoted in Richards 2010, p. 49); and Ereshefsky (2001, p. 95) holds the same view: “Prior to the acceptance of evolutionary theory, essentialism was the standard mode of classification in biological taxonomy. Such biologists as John Ray, Maupertuis, Bonnet, Linnaeus, Buffon, and Lamarck believed that the proper way to sort organisms into species taxa is by their species-specific essences (Hull 1965; Sober 1980; Mayr 1982, 256ff.)”. The section of Mayr’s 1982 book (*The Growth of Biological Thought*) that Ereshefsky highlights has the heading “The Essentialist Species Concept”, and the fact that the names he cites are those of very renowned thinkers shows how widespread this view has been. Another philosopher adhering to the Received View is David Stamos (2003, p. 22) who says that species essentialism “has enjoyed a long and distinguished history, being traceable back, broadly speaking, to the views of Plato and Aristotle on the one hand and the Book of Genesis on the other. The combination of these two traditions found its culmination in Carolus Linnaeus”.[4] A pithy encapsulation of the Essentialism Story in a biological publication is given by Ghiselin (2001) in an entry on species concepts in the *Encyclopedia of Life Sciences*: talking about taxonomy since Linnaeus, he says that “[i]t was supposed that ‘kinds’ of plants and animals are as immutable as are kinds of minerals. (. . .) A group was supposed to have what

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[2] It should be noted again that for Mayr typology is a synonym for essentialism, i.e. for the notion that there are necessary and sufficient (“essential”) properties that make an entity what it is. See also the quote from Ghiselin (2001) further below which is taken from a section headed “Essentialism or Typology”.

[3] In fact, Wilkins holds that John Dewey, whose philosophy was strongly influenced by Darwin and who emphasized (or overemphasized?) the contrast between pre-Darwinian and post-Darwinian thought, was in part responsible for the success of the Essentialism Story, particularly through his essay on Darwin’s influence on philosophy (Dewey 1910) (Wilkins 2009b, pp. 169 and 179).

[4] This passage is also quoted by Richards (2010, p. 19), but he gives the wrong year of the publication (2004 instead of 2003).

is called an ‘essence’ or ‘nature’ that made it what it is. Classification meant discovering this essence, and defining groups on the basis of supposedly ‘essential’ properties. Much of the history of evolutionary thinking reflects a struggle to get rid of what is called ‘essentialism’ or ‘typology’. Essentialism presupposes the reality of essences, leading people to think in terms of stereotypes and to screen out that which is unique or variable”.

There is thus believed to be, in other words, an unbroken direct tradition from Platonic and/or Aristotelian essentialism in Greek antiquity through the particularly influential taxonomy of Linnaeus in the eighteenth century up to the middle of the nineteenth century when Darwin overcame essentialism and introduced evolutionary thought. Although this seems, at least at first glance, like a plausible account, we now know that it is an oversimplification or even a historical myth, or, as Richards (2010, p. 207) puts it: “The virtues of the Essentialism Story are its simplicity, dramatic power and rhetorical value. The problem with this story is that it is largely false”.

Although there are forerunners in criticizing the Essentialism Story (Wilkins 2009b, pp. 185 and 190, explicitly names Paul L. Farber and Scott Atran;[5] Winsor 2003, p. 389, names almost a dozen more), it is particularly the historian of biology Mary P. Winsor to whom we owe a growing awareness that the simple plot of the Received View is largely wrong (Winsor 2001, 2003, 2006a, b).[6] Winsor (2006a, p. 149) admits that “For years I taught it myself, but now I am convinced that it is little more than a myth”. She traces the origin of this “myth” to the mid-twentieth century and to Ernst Mayr: “The essentialism story is a version of the history of biological classification that was fabricated between 1953 and 1968 by Ernst Mayr, who combined contributions from Arthur Cain and David Hull with his own grudge against Plato. It portrays the pre-Darwinian taxonomists as caught in the grip of an ancient philosophy called essentialism, from which they were not released until Charles Darwin’s 1859 *Origin of Species*. Mayr’s motive was to promote the Modern Synthesis in opposition to the typology of idealist morphologists; demonizing Plato served this end. Arthur Cain’s picture of Linnaeus as a follower of ‘Aristotelian’ (scholastic) logic was woven into the story, along with David Hull’s application of Karl Popper’s term, ‘essentialism’, which Mayr accepted in 1968 as a synonym for what he had called ‘typological thinking’. Although Mayr also pointed out the importance of empiricism in the history of taxonomy, the

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[5] Atran, who is perhaps best known for his analysis of folk biology and taxonomy across diverse human cultures, was indeed remarkably clear on this: “I have so far failed to find any natural historian of significance who ever adhered to the strict version of essentialism so often attributed to Aristotle. Nor is any weaker version of the doctrine that has indiscriminately been attributed to Cesalpino, Ray, Tournefort, A.-L. de Jussieu and Cuvier likely to bear up under closer analysis.” (Atran 1990, p. 85, quoted from Wilkins 2009b, p. 190). Interestingly, Atran does not list Linnaeus here, although the same applies to him, at least in his later years.

[6] Mary Winsor particularly discusses Linnaeus. Varma (2009) argues that Ernst Mayr’s description as an essentialist of a much less widely known biologist from the early 1800s, the entomologist William Kirby, is also an oversimplification.

essentialism story still dominates the secondary literature" (Winsor 2006a, p. 149). However, as worked out in some detail by Winsor herself (Winsor 2003, 2006b) as well as Wilkins (2009a, b) and Richards (2010), pre-Darwinian taxonomists were not at all driven by Platonic or Aristotelian essentialism (see Sect. 2.2), and, as a consequence, "Darwin was not confronted with anything like the assumed essentialism consensus", but with "a multiplicity of species concepts, based on similarity, fertility, sterility, geographic location and geologic placement and descent" (Richards 2010, pp. 17 and 75). Indeed, it can and has been argued that the Darwinian revolution had surprisingly little impact on taxonomy. The pre-evolutionary Linnaean system is still in use (repeated criticism notwithstanding, e.g. by Ereshefsky 2001; Bertrand et al. 2006; Laurin 2010; Zachos 2011; Lambertz and Perry 2015), and while the acceptance of evolution made species fixism scientifically untenable, it has not at all caused a revolution in taxonomic practice. Rather, the result of that taxonomic practice has since been interpreted in an evolutionary framework, and relationships have been reinterpreted as the result of common descent in the Tree of Life. But how, then, did the Essentialism Story come to be the standard view of the historical development of species concepts in biology? Winsor (2001, 2006a) gives a quite detailed reconstruction of what she believes to be the history of the creation of the Essentialism Story. Very briefly, according to this reconstruction, it started with Arthur Cain's 1958 paper *Logic and memory in Linnaeus's system of taxonomy* in which he portrays Linnaeus as an adherent of Aristotle' s logic of division and thus as a proponent of species having eternal essences (necessary and sufficient properties that make them what they are). Cain's (flawed) understanding of Aristotle, in turn, was based on a textbook on logic from 1916 by H. W. B. Joseph (but according to Wilkins 2009a, p. 1, note 2, this misconception of Aristotle was due to Cain, not Joseph). This is how Linnaeus became stigmatized as an Aristotelian or scholastic essentialist. Interestingly, much later, Cain revised his views on Linnaeus (e.g. Cain 1993, 1994; Winsor 2001; Wilkins 2009a cite further references), "but by then it was too late... Cain had let loose a genie that would prove very difficult to put back in its jar" (Winsor 2006a, p. 165). By this time David Hull and Ernst Mayr had followed Cain's tracks. Cain's 1958 article is cited in both Hull's 1965 essay on essentialism in taxonomy and in Mayr's *Growth of Biological Thought* (1982), and it has probably been the enormous success of the latter that has spread the Essentialism Story further.[7]

Even after the publications by Mary Winsor on the Essentialism Story, this version of taxonomic history keeps getting told or even defended (Ereshefsky 2010a; for a reply to Winsor, see particularly Stamos 2005). To me, however, the detailed reconstruction of notions about species through history by Wilkins (2009a, b) and Richards (2010) make a very convincing case that the Essentialism Story is at the very least an oversimplification of more than 2000 years of pre-Darwinian

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[7] A much more detailed reconstruction can be found in the papers by Mary Winsor cited in this chapter.

thought. There is also an ironic twist to the Essentialism Story: not only did naturalists of the pre-Darwinian era not blindly follow Aristotelian essentialism, but Aristotle himself did not either—at least not with respect to the living world which he realized could not be adequately described by the means of his logical methodology. This will be the starting point of the next section.

2.2 Species from Antiquity to Darwin

Having criticized the historiography as promoted by the Essentialism Story in the preceding section, this section aims at a more balanced and more substantiated depiction of taxonomic thought in the pre-Darwinian era. Perhaps the most important lessons to be learned from a short summary of the history of species thinking through this very long period are (1) that the early naturalists in the Renaissance and particularly in the seventeenth and eighteenth centuries were not caught in the stranglehold of essentialism but that the kind of Platonic and/or Aristotelian philosophy that the Essentialism Story imputes to them is the exception rather than the rule among pre-Darwinian biologists, and (2) that Aristotle's biology and his use of the term species (*eidos*) in it were very different from that in his works on logic and that the misrepresentation that followed from this difference was in large part due to the peculiarities of the reception of Aristotle in the era of Neoplatonism and medieval scholasticism.

Essentialism is usually traced back, via Aristotle, to Plato's theory of Ideas or Forms. To Plato the non-material eternal and immutable ideas (universals like general "redness" or the concept of a chair) were what was ultimately real, not the mutable and ephemeral world of particular objects that we perceive with our senses (like a red apple or the particular chair I am sitting on). The particular apple is red because it partakes of the general or universal idea of redness. This participation is called *methexis*. The world as we know it is only a flawed shadow (quite literally so in Plato's famous Allegory of the Cave) of the eternal and perfect world of Platonic ideas. It is this view—that the idea is real and unchanging and the variable instances of these ideas in the world of sensation are imperfect and less real entities—that Ernst Mayr called typology (for him synonymous with essentialism) and opposed to what he called population thinking where variability is real and the type or mean is only an abstraction. Both Plato and his student Aristotle tried to find the true meaning of things, their essence as it were. In fact, the word essence comes from Latin *essentia*, and this in turn goes back to Aristotle's somewhat mysterious expression *to ti en einai* (the "what it is to be" or "what it really is"). However, there were important differences. While Plato believed that universals like redness existed before and independently of their specific instances like a red object (*universalia ante res* as the Latin tag has it), to Aristotle the reality of universals lay within their instances (*universalia in rebus*). More importantly, Aristotle did not believe that classification should or could always proceed dichotomously as Plato wanted it. Classification of things (both living and nonliving) was performed by

Plato by means of a method called *diairesis* which literally means division but is often also translated as dichotomy because Plato's pattern of classification was strictly dichotomous. The *locus classicus* in Plato's work is the dialogue *Sophist* where angling is defined in a strictly dichotomous way from more general to ever more specific activities. This procedure of dichotomous classification is still familiar to biologists in the form of identification keys for different taxa. Although Aristotle disagreed with Plato on the need of dichotomous splits, his logic was often depicted as dichotomous as well because the Neoplatonic interpretation strove to reconcile Aristotle with Plato (and, later, both with Christianity). During the Middle Ages Aristotle was known as "the philosopher", and he was by far the single most authoritative source on philosophy and science, but although his work and thought were of perhaps unparalleled diversity, it was his logic that was most widespread and the basis of higher education. Also, it was not Aristotle's writings themselves (which were not directly known) but two works by Neoplatonic writers, Porphyry and Boethius, to which Aristotle largely owed his medieval fame. Porphyry of Tyre, probably a student of Plotinus, wrote an introduction (*Isagoge* or *Eisagoge* in Greek) to Aristotle's logic in the second half of the third century AD, which was then translated into Latin by Boethius in the first half of the sixth century AD. Boethius' translation was very widespread and influential in the Middle Ages. Through the *Isagoge* and its translation, the problem of universals (the question whether general properties like redness exist independently of their instances) was introduced to scholastic thinking, and Aristotelian reception was primarily the reception of his logical work. Porphyry's *Isagoge* was also translated into Arabic, Armenian and Syriac, and Aristotelian logic was an integral part of medieval education in the seven liberal arts (*septem artes liberales*).[8] In line with this, Wilkins (2009a, p. 5) holds that the "crucial medieval link between Aristotle and modern biology was not Linnaeus" but "the late classical neo-Platonists, rediscovered by the Cambridge Platonists [a group of philosophers and theologians at Cambridge University in the seventeenth century] (...) by way of their influence on John Ray, John Locke, and various other seventeenth-century notables". It was this *logical* tradition from which Linnaeus drew his categories, particularly genus and species (the Latin translations of the Greek *genos* and *eidos*), which did not have any specifically biological meaning during the preceding centuries. The Neoplatonic depiction of the Platonic–Aristotelian logic is best known from what later (through Peter Ramus in the sixteenth century) became known as Porphyry's tree (*Arbor Porphyriana*, Fig. 2.1). Porphyry's tree is a graphical representation of a top-down classification, beginning with the highest level, the *summum genus*, and going down to the lowest species, the *infima species*, which only contains individuals or particulars but no further general entities (universals). The overall pattern is encaptic or nested, with more inclusive entities at the top and less inclusive further down. Except for the highest and the lowest, all levels are species with respect to

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[8] For this and the role of Porphyry and Boethius see, for example, Flashar (2013), pp. 207, 355, 362, Marenbon (2013) and Emilsson (2015).

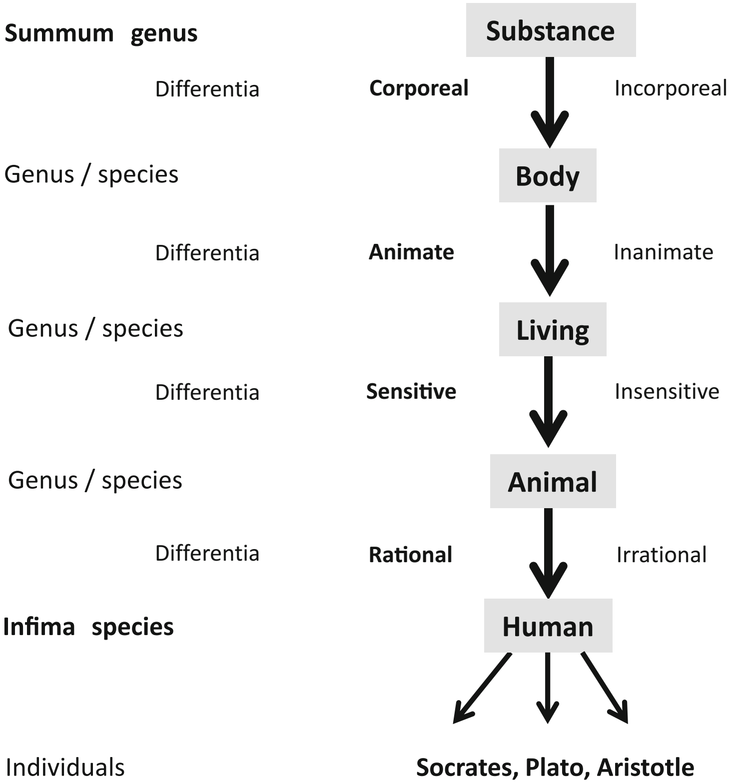

Fig. 2.1 Porphyry's tree as exemplified by the classification of humans. The substance is the highest genus (*summum genus*), i.e. it is not at the same time a species to an even higher genus. By means of particular differences (*differentiae*), a genus is split up dichotomously into species. The first dichotomy of *differentiae* is corporeal vs. incorporeal (here and further down in the classification the *differentiae* whose path the classification follows is in bold, the alternatives on the far right in normal print). All corporeal substances are bodies. Body is a species with respect to its genus (substance), but it is a genus with respect to the next lower level (living beings) which is arrived at through the dichotomy animate vs. inanimate. The lowest species which is not further divisible into subordinate species but only into individuals, i.e. which is not a genus with respect to a lower level, is called the *infima species*. Thus, except for the highest (*summum genus*) and lowest (*infima species*) levels, genus and species are relative terms. This kind of classification is still being practised, for example, in biological identification guides which are often based on dichotomous keys down to species level. Porphyry's tree is also reminiscent of cladograms, which are based on dichotomous splitting as well

higher and genera with respect to lower levels. Each genus is subdivided into species based on particular differences (*differentiae*; *diaphora* in Greek).

So much (or rather so little) for the reception of Aristotelian logic. The Essentialism Story basically projects this logical pattern with essential properties of logical species (being rational is a necessary and sufficient condition of the species human) onto biological species and claims that this was the main view on biological species until Darwin came and got it right. However, this is an oversimplification and does an injustice to many pre-Darwinian biologists—including Aristotle to whom we purportedly owe this essentialist misconception of species.

As already mentioned above, Aristotle himself was a much better and much more empirical biologist than this tradition might suggest, and he has been given credit for it by very eminent biologists. Richard Owen said about Aristotle's significance for biology that "Zoological Science sprang from his labours, we may almost say, like Minerva from the Head of Jove, in a state of noble and splendid maturity" (Owen 1992, p. 91, quoted from Lennox 2014, p. 1); and Darwin famously wrote to William Ogle (the English translator of Aristotle's *De Partibus Animalium*) in 1882, shortly before his death, "From quotations which I had seen I had a high notion of Aristotle's merits, but I had not the most remote notion what a wonderful man he was. Linnaeus and Cuvier have been my two gods, though in very different ways, but they were mere school-boys to old Aristotle" (quoted from Gotthelf 1999, p. 4).[9]

In particular, Aristotle's use of the term species (*eidos*) in his biological works—which take up more than one fourth of his total oeuvre—is very different from his logical species. I will only briefly summarize this issue here which is dealt with in detail by Wilkins (2009a) and Richards (2010). A short technical overview of Aristotle's biology can be found in Lennox (2014). The same author (Lennox 2001) has also published a more comprehensive work on this topic, and there is a very recent book by a renowned biologist as well (Leroi 2015).

While in his logic essential properties occurred, and although he often used animal examples to illustrate logical divisions, Aristotle "did not use that method in his biological work to systematically classify organisms into species kinds. Nor did he seem to think that the method could be so used" (Richards 2010, p. 24; see also Lennox 2014). Aristotle used the term species (*eidos*) in at least three senses: (1) as logical universals, (2) as enmattered form and (3) as principles of development and organization (Richards 2010, p. 47). Only the first of these is the species of Aristotle's logic as found in the *Categories* and *On Interpretation*; the other two are fundamentally different and used in his biological works: "the term *necessary conditions*, refers to what we might describe as the *functional and developmental conditions* required for a certain kind of life, rather than the *logical conditions* of a taxonomic definition. (...) Aristotle did not see essences as the basis for species groupings in the modern sense. He saw them as the basis for understanding the functioning, development and flourishing of organisms in environments. Essential properties are necessary for a particular lifestyle in an environment. Accidental properties are not. This is clearly not the property essentialism orthodoxy usually attributed to Aristotle, for it does not involve using his logic of division to arrive at *definitions* of animal species kinds expressed in terms of their intrinsic properties" (Richards 2010, p. 27f.). Rather than a property or material essentialist (essence as

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[9] Gotthelf (1999) emphasizes that this is not just politeness or lip service but that Darwin was indeed deeply impressed by Aristotle's biological works.

physical properties), Aristotle was a teleological essentialist: essences were a power to achieve an end—for organisms, essence was life itself, for animals it was a life of sensation and self-movement and, for humans, rationality that came on top of that (Ereshefsky 2001, p. 18, after Lennox 1987 and Ayers 1981).

The focus on Aristotle's logical works and its meaning of species/*eidos* made "Aristotle look as if he were a property essentialist. Since philosophers from late antiquity to the late medieval period, typically began and ended their study of Aristotle in the works on logic, it is no surprise that they read Aristotle in the manner of the Essentialism Story" (Richards 2010, p. 31). One of the first to state this misinterpretation of Aristotle's species was Scott Atran (see also Sect. 2.1): "A major source of error in the interpretation of natural history is thus owing to a misleading analysis of Aristotle's Logical Division that has been unduly influenced by the idealism of some of the Oxford scholars, most notably H.W.B. Joseph (1916). Such analyses tend to maintain that Aristotle accepts the parallelism between the division of geometrical forms and those of biological kinds as a matter of observed fact… But everything in Aristotle's biological works indicates this is not so" (Atran 1990, p. 87, quoted from Winsor 2001, p. 250).[10]

Aristotle did not practice the kind of property essentialism in his biology that the Received View imputes to pre-Darwinian thinkers. But of course the fact that he was misinterpreted does not mean that others who followed him were not property essentialists with respect to biological species either. So, were they? Obviously this must be decided on a case by case basis, but it seems fair to generalize that pre-Darwinian biologists were much less affected by logical essentialism than often claimed. Rather than viewing species as endowed with essential properties, there was from early on (since the Epicureans, according to Wilkins) a notion which Wilkins calls "the generative conception", the "marriage of reproduction or generation, with form" (Wilkins 2009a, p. 10), i.e. "that natural or living species have a generative order or power that makes progeny resemble [parents],[11] and development to occur in a repeated orderly sequence" (Wilkins 2009b, p. 18). And indeed, beyond interfertility, adaptation, ecological niches, etc., what combines all notions on species is genealogy and a certain degree of similarity. This is already encapsulated in Aristotle's slogan that "it takes a man to generate a man" and can be found in many definitions of species ever since, e.g. in Cuvier (1812) when he says that species are "those individuals which descend from one another, or from common parents, and those which resemble them as much as they resemble each other".[12]

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[10] Wilkins holds that it was not Joseph's but Cain's misconception; see Sect. 2.1.

[11] Instead of parents it says "children" in the original, but I am sure this is a mistake and use parents here.

[12] Translated from Cuvier (1812), Recherches sur les ossemens fossiles de quadrupèdes. Discours préliminaire, p. 74, accessed at http://www.lamarck.cnrs.fr/ice/modules/ice2pdf/pdf/extraitPDF08-03-2016_16-27-12.pdf on 8 March 2016: "les individus qui descendent les uns des autres, ou de parens communs, et ceux qui leur ressemblent autant qu'ils se ressemblent entre eux"

The natural history tradition as we know it began in the Renaissance of the mid-fifteenth century, and the study of medicinal plants was an important trigger. Well-known Renaissance “biologists”[13] of the fifteenth and sixteenth centuries were Niccolo Leoniceno, the three “fathers of botany” (Leonhart Fuchs, Otto Brunfels, Hieronymus Bock), Conrad Gesner, Ulisse Aldrovandi and, most importantly, Andrea Cesalpino. Cesalpino was indeed influenced by Aristotelian logic, disregarding (or rather being unaware of) Aristotle’s rejection to apply it to the biological realm, and he distinguished underlying essences (but used the Latin word substances here) from accidentally varying characters in species (Wilkins 2009a, p. 56f.; Richards 2010, p. 53f.). His use of reproductive traits for botanical classification influenced later researchers, most notably John Ray and Linnaeus (ibidem). According to Wilkins (2009a, p. 65f.), it was John Ray who first defined species in a truly biological context.[14] In the first volume of his *Historia Plantarum* (The History of Plants), he writes in 1686 about species definition: “no surer criterion has occurred to me than the distinguishing features that perpetuate themselves in propagation from seed. Thus, no matter what variations occur in the individuals or the species, if they spring from the seed of one and the same plant, they are accidental variations and not such as to distinguish a species…Animals likewise that differ specifically preserve their distinct species permanently; one species never springs from the seed of another nor vice versa” (quoted in Mayr 1982, p. 256f.). A number of things are important here. Although Ray applied the term species also to metals (as Linnaeus did to minerals), this is indeed a much more “biological” definition than previously had been advanced. It is also a definition that highlights genealogy (descent) and reproduction and thus is much more in line with Wilkin’s idea of a generative conception of species than with a logical treatment of species membership that hinges on essential traits. In point of fact, the juxtaposition of genealogy (“springing from the same seed”) and the “accidental variations” (a term obviously showing the logical tradition of essential and accidental properties) suggests that, if at all, genealogy functions as something like a species’ essence, but this “essence” is very different from the kind of property essentialism that the Essentialism Story takes for granted. Finally, Ray highlights the problem of

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[13] Like everywhere else in this book, I call everybody a biologist who is dealing with what we today know as biology. The sundering of natural history into today’s scientific disciplines (biology, palaeontology, geology, mineralogy) is of course a relative young phenomenon, and the term biology in its modern meaning was not used before the middle of the eighteenth century and did not come into general use before ca. 1800 (Toepfer 2011, vol. 1, p. 254).

[14] Nonetheless, Wilkins (2009a, pp. 39ff., 2009b, p. 21f.) also notes a very peculiar and noteworthy medieval outlier: Frederick II of Hohenstaufen. In his book *De arte venandi cum avibus* (The Art of Hunting with Birds), published in the middle of the thirteenth century, Frederick distinguished between what a species is and how it can be identified and emphasized intraspecific variability and the ability to interbreed as the mark of species. Wilkins concludes (2009a, p. 41): “The way he refers to species is so clearly in line with modern usage that he might be considered to have been the first to give a truly biological account”. However, while he definitely serves to show that thinking about species was far more diverse than often depicted, he is also an exception with respect to his “modern” views.

fuzzy boundaries and “ceases to expect that there will be sharp demarcations between species” (Wilkins 2009b, p. 37): “Nature, as the saying goes, makes no jumps and passes from extreme to extreme only through a mean. She always produces species intermediate between higher and lower types, species of doubtful classification linking one type with another and having something in common with both” (in Wilkins 2009b, p. 38, from Ray’s 1682 *Methodus plantarum nova*, quoted in Glass 1959, p. 35). Both Wilkins and Richards highlight that an important development was the fusion of a genealogical notion of species with theological assumptions about their creation (e.g. Richards 2010, p. 197). Indeed, viewing species as genealogical lineages is easily compatible with tracing them back to an act of creation. Wilkins (2009a, p. x, 93ff.) even holds that species fixity was invented by John Ray (and repeated by Linnaeus) but that whenever it occurred it was a concession to piety and not rooted in scientific reasoning.

A reproductive lineage conception of species can also be found in Buffon who has been cited by Ernst Mayr (1996, p. 269) as a forerunner of “his” Biological Species Concept.[15] It is not quite that easy, though, with Buffon. Like many others, Buffon made various and sometimes contradictory comments on species and seems to have changed his views over time (Richards 2010, p. 62ff.; Wilkins 2009a, p. 75ff., 2009b, p. 43f.). He published his *Histoire Naturelle, Générale et Particulière* between 1749 and 1788 in 36 volumes (eight more volumes appeared posthumously), and in the beginning he denied the existence of species claiming that only individuals existed and that species were just a convention—an early example of species taxon nominalism—but soon after introduced a reproductive criterion based on fertile offspring (hence Mayr’s praise for him) *and* the preservation of likeness of the species through time, and he engaged in fertility experiments. He also proposed some kind of evolutionary change, albeit one constrained by an internal mould (*moule intérieur*). Drawing on a number of authors (Sloan, Farber and Lovejoy), Wilkins (2009b, p. 43) summarizes Buffon’s position as follows: “He had two distinct periods of views of species—one in which they were Lockean conveniences, and one in which they were defined by mutual sterility (. . .) His ‘biological’ definition is not, as Mayr and others said, purely about interfertility, but also about the generation of progeny that are similar to their parents. . .his ‘species’ is more akin to the Linnaean genus or higher, so reproductive interfertility is much broader on his view than the modern biospecies conception. He believed that Linnaean species evolved by degeneration and the action of habit and soil from a ‘primary stock’ (première souche), and so, for example, all great cats were a single species that could be backbred to the original stock”.

Buffon’s views strongly influenced Immanuel Kant who, in 1775 in his essay *Von den verschiedenen Racen der Menschen* (Of the Different Human Races),

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[15] In fact, Mayr (1996, p. 269) calls “his” forerunners “prophetic spirits” because they “foreshadowed a different [his own] species concept, later designated the biological species concept (BSC)”. Wilkins (2009a, p. 194f. and note 13) criticizes this as a doubtful way of backing up one’s own views with the allegedly similar views of past greats (“Whig interpretation of history”).

wrote: “In the animal kingdom the division of nature into genera and species is grounded on the general law of reproduction, and the unity of the genus is nothing else than the unity of the generative force, which is considered as [continuously/universally] active for a determined manifold of animals. Thus, the Buffonian rule—that animals which can generate fertile young and which might show differences in form, belong to one and the same physical genus—can properly be applied only as the definition of a natural genus of animals generally, to differentiate it from all logical genera. The logical division proceeds by classes according to similarities; the natural division considers them according to the stem and divides animals according to genealogy, and with reference to reproduction. One produces an arbitrary system for the memory, the other a natural system for the understanding. The first has only the intention of bringing creation under titles; the second intends to bring it under laws”.[16]

Kant’s view is interesting for a variety of reasons. First, it is very clear that genealogy trumps similarity in a natural approach; there is again a notion of a lineage here. Second, the “unity of the generative force” is reminiscent not only of Buffon (and, indeed, Ray, Wilkins 2009a, p. 86) but also of Aristotle’s particularly biological use of *eidos*. Third, Kant’s distinction between natural and logical genera/species and classification (the German terms are *Naturgattung* vs. *Schulgattung*), which is also found in Buffon, shows that naturalists and philosophers indeed were aware (just like Aristotle) that logic was not applicable in the same way to natural history as it was to other branches of science. This distinction is also somewhat reminiscent of the one between T (taxonomic) and E (evolutionary) species made in Sect. 1.3.2 in that the logical unit, just like the T species in many cases, is a necessary classification for practical reasons, whereas the natural unit and the E species actually capture a non-arbitrary part of extramental reality.

Even more famous and influential than Buffon and often regarded as the true father of modern biological taxonomy and classification is his contemporary Carl Linnaeus. He is also one of the prime suspects of taxonomic essentialism. Particularly due to Mary Winsor (see Sect. 2.1), there is a growing awareness that Linnaeus was not simply an essentialist. But what, then, was his view on species? Very importantly, there was no single view in Linnaeus. He fundamentally changed his notion of species later in life. His classification scheme based on what is now known as the Linnaean categories was inspired by the Neoplatonist and scholastic tradition of Aristotelian logic (Wilkins 2009a, p. 70f.). His *Systema Naturae* (first edition in 1735) distinguished five such categories: kingdom (regnum), class (classis), order (ordo), genus and species, with the kingdom being equivalent to the *summum genus* and the species being the analogue of the *infima species* (see

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[16] Translation from Sloan (1979). I have left out the German terms that Sloan sometimes gives, and I have changed his translation of the German “durchgängig” from “generally” to “continuously/universally” to make it clear that Kant’s original (Kant 1998, p. 11) does not allow for exceptions. The fact that Kant often uses genus where we would expect species is because he did not consider these two terms to be different in the context of natural history (Sloan 1979).

Fig. 2.1). At that time, he thought of species as fixed, discrete and timeless, and no new species were ever produced. His famous definition of species, which, however, may owe just as much to piety as to science (Wilkins 2009a, p. 72), is that "there are as many species as the Infinite Being produced diverse forms in the beginning" (*species tot sunt diversae quot diversas formas ab initio creavit infinitum Ens*) (ibidem). Linnaeus was thus a special creationist, believing in the creation of every single species by God. However, Linnaeus was far too good a biologist to not realize that his species fixism was not in accordance with his empirical findings and that species were not immutable.[17] He had this brought home to him in 1742 when he was shown a specimen of the common toadflax (*Linaria vulgaris*) with an aberrant flower that he described as *Peloria* (literally a monstrosity, from the Greek *pelor* for monster) and compared to a calf born with a wolf head (Hagberg 1940, p. 221ff.; Gustafsson 1979). According to Hagberg, "Linnaeus was in a state of perplexity with respect to species" at the end of the 1750s, and although he never gave an explicit definition of his new view on species, he had abandoned his old one of immutable species (Wilkins 2009a, p. 73). He "removed the statement that there were no new species from his 1766 edition of the *Systema Naturae* and crossed out the statement natura non facit saltum from his own copy of his *Philosophica Botanica*" (ibidem). In particular Linnaeus allowed for what is today known as hybrid speciation (and carried out hybridization experiments). His new insights were also included in his *opus magnum*: "In the tenth edition [of the *Systema Naturae*] of 1758, he wrote that God created an original individual or mating pair for each genus and that new species were produced by inter-generic crosses. In the thirteenth edition of 1770, he speculated that the original breeding pairs or individuals might instead represent *orders*, rather than *genera*, and that even new genera, as well as species, might be formed through hybridization" (Richards 2010, p. 58).

While holding on to divine creation, Linnaeus was forced to let in evolution "through the back door" by increasing the hierarchical level at which creation sets in and by allowing for everything below this level to come into existence through natural processes. Richards (2010, p. 59f.) nicely summarizes Linnaeus's later views and argues against the kind of essentialism in his thinking that the Essentialism Story imputes to him: "if he was an essentialist, it was of a *genealogical* kind. Essences were passed on in reproduction via the transmission of medullar matter [[18]]. But he was clearly not a *property* essentialist in the standard philosophical sense (. . .) whatever essences there were, were not associated with any particular set of physical, intrinsic properties! (. . .) in Linnaeus's genealogical essentialism, an organism was a member of a species not because of a set of properties, but because of genealogy. Lurking here is the idea that species are lineages (. . .) by his

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[17] See also Müller-Wille (2001) who comments on Linnaeus's species concept in the context of eighteenth-century botanical practice and gives a short list of relevant literature on Linnaeus.

[18] Linnaeus thought that there were a female medulla (responsible for life itself) and a nourishing male cortex that were passed on to the next generation through reproduction, a notion that ultimately goes back to Aristotle who held similar views.

use of binomial nomenclature to name kinds and list of descriptive traits to identify them, Linnaeus may look like an essentialist committed to Aristotle's logic of division. In his taxonomic tables, he could have been doing something like giving definitions for fixed, unchanging and discrete species. But his views about the origins of species paint a very different picture, a picture of species formation from an apparently unlimited process of mixing that constantly produces new forms out of old, and forms not necessarily well-defined and discrete". This is in line with Mary Winsor who holds that to Linnaeus "essential" characters only meant taxonomically useful characters and who points out that the fact that Linnaeus attached *absolute* ranks to the terms genus and species (which are relative terms in logic, see Fig. 2.1) "proves his utter disregards for the 'Aristotelian' rules of logic" (Winsor 2006a, b, p. 5). To understand the potential contradiction between Linnaeus' taxonomic system that at least resembles a logical system and his view on species or even higher taxa and the natural processes that produced them, it is important to remember that he did not consider his own system as natural (i.e. complete and revealing God's ideas). *Essential* characters to Linnaeus were somewhat like a shortcut to distinguish one taxon from others in the natural order, but ultimately only *natural* characters, i.e. a full list of all features, would reveal a truly natural system, and he even explicitly warned against jumping to conclusions based on the knowledge of only essential characters (Winsor 2006b).

Summing up the development from Ray to Linnaeus and Buffon, Richards (2010, p. 69) says that "there was a turn to a historical and genealogical conception of species. Members of a species were connected through reproduction into lineages that stretched back to the Creation". However, at the same time, when it came to species *identification* (not definition) in practice, classification was often similarity-based (ibidem). This can perhaps best be seen in Linnaeus, but it is still largely valid today.

Unlike Cuvier who was a convinced species realist and rejected species transmutation, the perhaps first real evolutionist, Lamarck, was very much in the tradition of *scala naturae* thinking and the (early) views of his teacher Buffon that only individuals exist and that species are human abstractions. The *scala naturae* or great chain of being is a philosophical conception of nature as an ascending ladder from inanimate objects through all forms of life (with humans at the top, of course) and then on via angels to God. This very influential idea goes back to Plato and Aristotle and is ultimately a combination of two metaphysical principles: (1) that everything that can possibly exist does exist (principle of plenitude) and (2) that transitions in nature are continuous, i.e. that there are no gaps in the chain of being (principle of continuity, famously encapsulated as *natura non facit saltus*, "nature does not make jumps").[19] The best-known version of the *scala naturae* in biology is the *échelle des êtres naturels* of the eighteenth-century Genevan naturalist Charles Bonnet (see, e.g. Rieppel 2001), and Lamarck

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[19] The classical magisterial treatise on the *scala naturae* from scientific, philosophical and cultural perspectives is Lovejoy (1936).

interpreted this chain temporally in a progressive and orthogenetic (directed) evolutionary framework, also allowing for branching events to make it more realistic (e.g. Bowler 1989, pp. 82–88). Lamarck took the principle of continuity very seriously and therefore was a nominalist with respect to species, i.e. he denied the objective existence of species and also of extinction (except when human-caused) because in his view fossil forms evolved into present species (ibidem, Wilkins 2009a, p. 107).

Another early nineteenth-century biologist, Augustin-Pyramus de Candolle, provided a neat species definition and yet another piece of evidence that property essentialism was not the rule in taxonomy. To him a species was “the collection of all the individuals who resemble one another more than they resemble others; who are able, by reciprocal fecundation, to produce fertile individuals; and who reproduce by generation, such kind as one may by analogy suppose that all came down originally from one single individual” (Wilkins 2009b, p. 66, quoted from Hunter Dupree 1968, p. 54). This is a very interesting definition as it combines the three criteria that even today are most often used in species description and delimitation: similarity, interfertility or gene flow and common descent. The emphasis, once again, of similarity and genealogy confirms Wilkins’ claim that his generative notion of species has been the most widely used since antiquity.

That said, were there no species essentialists at all that fit the description of the Essentialism Story? Yes, there were, but only very few. According to Wilkins (2009a, p. 69, 93), the possibly only true material or property essentialist before the nineteenth century was Nehemiah Grew, a contemporary of John Ray in the seventeenth century. Charles Lyell may have had some essentialist tendencies (Richards 2010, p. 69) but it is debatable whether his views really were of the kind that the Essentialism Story deals with. Those of the widely read Philip Henry Gosse, however, definitely were (Wilkins 2009a, p. 118f.). In his famous book *Omphalos*’ he says: “I assume that each organism which the Creator educed was stamped with an indelible specific character, which made it what it was, and distinguished it from everything else, however near or like. I assume that such character has been, and is, indelible and immutable; that the characters which distinguish species from species *now*, were as definite at the first instant of their creation as now, and are as distinct now as they were then” (Gosse 1857, p. 111). He was not a professional scientist, though, and is therefore certainly not a representative of the scientific thought of his day. This then leaves us with one of Darwin’s contemporaries—Louis Agassiz. He seems to be the only important biologist to really be in accordance with the Essentialism Story. Agassiz, like his teacher Cuvier, believed in the constancy of species and “was indeed a Platonist who considered species thoughts in the mind of God, and he was also undoubtedly a species fixist, particularly after Darwin. Moreover, he was both a taxonomic essentialist and a material essentialist. Possibly he was the *first* such essentialist fixist Platonist” (Wilkins 2009a, p. 115). He also thought that individual organisms did not completely instantiate the types or ideas that species were (Wilkins 2009b, p. 61). This is as Platonic as taxonomy and biology can be. But Agassiz’s views were by no means representative or typical, and according to Amundson (2005,

p. 79, cited in Wilkins 2009a, p. 114f.), Mayr's detailed knowledge of Agassiz's work at the Museum of Comparative Zoology at Harvard (which was founded by Agassiz and of which Mayr became the director) biased his views towards a predominance of essentialism in taxonomy. As shown by the brief summary in this chapter and much more so by the in-depth publications by Winsor, Wilkins and Richards, this predominance of essentialism in all likelihood never existed. Rather, "essentialism, construed as the claim that a general term or concept must have necessary and sufficient inclusion criteria, is a long-standing *formal* notion, but when it comes to applying that notion to living things, it was always understood that living species were a different category to formal species" (Wilkins 2009a, p. 89).

Instead of having to fight Platonic or Aristotelian essentialism, Darwin thus found himself in a very different situation: "Naturalists used many criteria for identifying species, but all agreed that genealogy was most important" (Richards 2010, p. 198). Darwin was well aware of this when he wrote in the *Origin*: "With species in a state of nature, every naturalist has in fact brought descent into his classification (. . .) He includes monsters; he includes varieties, not solely because they closely resemble the parent-form, but because they are descended from it" (Darwin 1859, p. 424). Unfortunately, as will be seen in the next section, not all of Darwin's comments on species were so unequivocal.

2.3 Darwin and the Species Problem

Whenever it comes to Darwin, things get complicated. Firstly, because he is the single most analysed and written about biologist (perhaps even scientist in general), and getting an overview of the available literature is all but impossible. Secondly, he is such an admired thinker that to be able to show that "already Darwin said so" seems to bestow authority on and reinforce one's own views (there is an ironical parallel to Jesus here). Given that Darwin was wrong on a number of topics (most famously perhaps on the mechanisms of inheritance), as one would expect with someone or indeed anyone who worked almost two centuries ago, this seems a somewhat odd line of reasoning. Darwin's views on species, what they are and whether they are objectively real, are particularly contentious, and there is even a long-standing argument about whether the title of his great book is inadequate because it allegedly does not deal with the origin of species and speciation but more with other topics such as evolution in general and natural selection (see Mayr 1982, p. 412ff.; Wilkins 2009a, p. 130 objects vehemently[20]). In this section I will only give a very short summary of Darwin's probable views on species and his impact on post-Darwinian taxonomy; more detailed discussions can be found in Wilkins

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[20] Wilkins (2009b, p. 105) thinks that the originator of this view is George Romanes, Darwin's assistant shortly before his death, who said that the theory of natural selection was not about the origin of species but instead about the origin of adaptations.

(2009a), Richards (2010), Ereshefsky (2011) and Stamos (especially in his 2007 book, but also in Stamos 1996, 1999, 2003, 2013). Wilkins (2009b, pp. 77–96) gives extended quotations from Darwin's writings on the topic. Because the use of the term species is often ambiguous—species taxa vs. species category, talking about taxonomic practice (T species) is different from talking about species lineages in the evolutionary process (E species)—one thing should become very clear: one cannot pick out a single of Darwin's quotes and draw general conclusions from it. Look, for example, at the following quotations (first from the *Origin of Species*, then from Darwin's letters):

1. "No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species" (Darwin 1859, p. 44; one might add that this is still very true today!).
2. "Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow" (Darwin 1859, p. 47; this is very similar to the Taxonomic or Cynical Species Concept, see Chap. 4).
3. "I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, and for mere convenience sake" (Darwin 1859, p. 52).
4. " I believe that species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links" (Darwin 1859, p. 177).
5. "Systematists will have only to decide (not that this will be easy) whether any form be sufficiently constant and distinct from other forms, to be capable of definition; and if definable, whether the differences be sufficiently important to deserve a specific name. (...) Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected. (...) In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species" (Darwin 1859, p. 484f.).
6. "no certain criterion can possibly be given by which variable forms, local forms, sub-species, and representative species can be recognized" (Darwin 1872, p. 38).
7. "fertility of their mongrel offspring...for it seems to make a broad and clear distinction between varieties and species" But then a little further down, he relativizes this: "It can thus be shown that neither sterility nor fertility affords any certain distinction between species and varieties; but that the evidence

from this source graduates away" (Darwin 1995, p. 246, 248); and ultimately arrives at this: "we may conclude that fertility does not constitute a fundamental distinction between varieties and species when crossed" (Darwin 1872, p. 259).

8. "I have just been comparing definitions of species, and stating briefly how systematic naturalists work out their subjects. (. . .) It is really laughable to see what different ideas are prominent in various naturalists' minds, when they speak of 'species'; in some, resemblance is everything and descent of little weight—in some, resemblance seems to go for nothing, and Creation the reigning idea—in some, descent is the key,—in some, sterility an unfailing test, with others it is not worth a farthing. It all comes, I believe, from trying to define the undefinable" (Darwin in a letter to Joseph Hooker, dated 24 December 1856, quoted from Darwin 1887, p. 88).
9. "How absurd that logical quibble—'if species do not exist how can they vary?' As if any one doubted their temporary existence?" (Darwin in a letter to Asa Gray, dated 11 August 1860, quoted from Darwin 1887, p. 333; Darwin refers to a criticism raised by Louis Agassiz).
10. "The power of remaining for a good long period constant I look at as the essence of a species, combined with an appreciable amount of difference; and no one can say there is not this amount of difference between primrose and oxlip" (Darwin in a letter to Joseph Hooker, dated 22 October 1864, quoted from Darwin and Seward 1903, p. 252).

Having read these statements, it is not surprising to learn that Darwin's real view on species has been hotly debated. While it is, like basically everything concerning Darwin, of high interest to historians of science, it should be noted that Darwin's views are of course not by definition superior to anybody else's, i.e. whatever he thought about species (inasmuch as his views can be unequivocally reconstructed) may also have been simply wrong, or at least he may at times have been just as inconsistent when talking about species as today's biologists often are. Two questions are particularly interesting: (1) Did Darwin consider species to be real natural units (species realism) or just constructs of the human mind that we use to artificially order biological diversity (species nominalism)? (2) What and how deep was Darwin's influence on taxonomy and systematics? To answer the former question, it is essential to remember the difference between the species *taxon* and the species *category*; the answer to the latter question hinges on whether pre-Darwinian taxonomy is overall considered to be essentialist or not.

The above quotes 3 and 5 in particular seem to suggest that Darwin was a species nominalist, viewing them as human constructs (and there is a long tradition of this interpretation, see Stamos 2007, Chap. 1 and Stamos 2003, p. 51ff.[21]). However, this is at odds with other quotes and the way he treated species throughout his work.

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[21] For example, Stamos (2003, p. 54) quotes Elliott Sober (1993, p. 143) who suggested that Darwin's *opus magnum* should more accurately be called "*On the Unreality of Species as Shown by Natural Selection*".

The usual solution to this apparent contradiction is to conclude that Darwin was a realist with respect to the species *taxon*, but a nominalist with respect to the species *category*, i.e. taxa like *Homo sapiens*, tigers or ginkgo trees were real to him, but the rank species was not. To him, there was no essence to the class of species taxa by which they could be unequivocally distinguished from varieties or other ranks. This is the view found, for example, in Wilkins (2009a, p. 156, 158, 2009b, p. 77), Richards (2010, p. 86ff.) and Ereshefsky (2010a, 2011): "We have seen repeatedly that Darwin did not insist *species* were unreal, merely that the *rank* was arbitrarily assigned (. . .) The reason why the term *species* has no discoverable essence (. . .) is that each case is different in the biological particulars. But they are separated, he says, in that the 'intergradations' between them are extinct. *That* is real enough" (Wilkins 2009a, p. 156).

What separates species from varieties is therefore ultimately a convention where along this continuum one draws the line. This is not to say that distinct lineages do not exist and do not evolve separately; rather, it is again the fuzziness of nature that blurs boundaries and creates grey areas. Richards (2010, p. 89ff.) thinks that according to Darwin there are five criteria by which species and varieties can be distinguished (morphological distinctness, morphological difference, morphological constancy, fertility/sterility, and geographic distribution) but for all these criteria species and varieties differ in degree, not in kind! Richards (2010, p. 89) also holds that for Darwin "whether a difference is relevant to the species-variety distinction depended on its implication for the history—the evolutionary fate—of the group of organisms". Whether Richards deliberately chose the expression "evolutionary fate" or not, the similarity to the view of the Evolutionary Species Concept is obvious, and that is perhaps not surprising because systematists have always granted taxonomic status only to non-ephemeral units, and Darwin would be no exception here.

With regard to the species category, Darwin seems to have been a pluralist, i.e. he thought that the real species taxa are not all the same kind of taxon but that there are different kinds of taxa, and Ereshefsky (who is himself a species category pluralist) reminds us that this view is still very much alive today (Ereshefsky 2011). Although he clearly has pluralistic tendencies as to what makes the species category, "all these causes resolve down to an aversion to interbreeding in sexual organisms and differences in their sexual structures and constitutions, and selection maintaining the appropriate forms and organs for living in the conditions in which they find themselves, for asexuals" (Wilkins 2009a, p. 158).

It should also be kept in mind that Darwin, just like biologists today, may have used the term species differently when talking about taxonomy and classification on the one hand (T species) and evolutionary biology on the other (E species). This is also the way that Wilkins sees it: "he [Darwin] has in fact a fairly orthodox view of species as real things in nature (albeit temporary things) (. . .) his dismissive comments in the Origin have more to do with the professional nature of taxonomy and the difficulties of diagnosis and nomenclature than a claim that species did not exist at all" (Wilkins 2009a, p. 129); and "Darwin was a species realist but denied the absolute rank of Linnaean classification, although he used it in practice and was a contributor to the Strickland Rules[[22]]" (ibidem, p. 158).

While species taxon realism and species category nominalism is perhaps the standard interpretation of Darwin's views, it is by no means unobjected. Particularly David Stamos has argued that Darwin was a realist with respect to *both* species taxa and the species category (Stamos 1999, 2007, 2013). He reconstructs what he believes to be Darwin's species concept (i.e. his definition of the species category) like this: "a species is a primarily horizontal similarity complex of organism morphologies and instincts distinguished at any one horizontal level primarily by relatively constant and distinct characters of adaptive importance from the viewpoint of natural selection, and secondarily (though not always applicable) by common descent and intermediate gradations" (Stamos 2007, p. 127, italics in the original). Since the species category (and with it all species taxa as its elements) is subject to natural laws, particularly natural selection, it is viewed as real, so the argument goes (see also Stamos 2003, p. 73). Stamos presents a scholarly in-depth analysis of Darwin's views on species. And he not only thinks that Darwin believed in the reality of the species category, but he also provides an explanation for the obvious objection that this would contradict many of Darwin's known statements. He attributes a strategy to Darwin that is supposed to explain the contradictions (Stamos 2007, Chap. 8).[23] Darwin is supposed to have used a sort of *reductio ad absurdum* strategy: he knew that his contemporaries believed in the reality of species (as results of the Creation) but rejected the reality of varieties. But if varieties and species turn out to be basically the same kind of thing, species could not be real either. This was then supposed to make his contemporaries change their concept of both varieties and species. Darwin further used species nominalism language until his sceptics were at least partly converted to his views, only to then switch to realism. Put this briefly, it may sound somewhat contrived but Stamos does give examples from Darwin's correspondence with Gray, Hooker, Lyell and Huxley.

So, was Darwin not just a species taxon but also a species category realist? The problem with Stamos's strategy theory is twofold. Firstly, it relies on Darwin viewing species mainly as horizontal entities (just like, incidentally, Stamos himself), but this may not have been the case. Descent featured prominently in Darwin's view on species, and Richards (2010, p. 73) consequently says that to Darwin (and many others like Ray, Buffon, Linnaeus and Kant) the criterion of

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[22] The Strickland Code (Strickland 1843), as it became known, is an early attempt at standardizing zoological nomenclature. The driving force behind it was Hugh Edwin Strickland (1811–1853), and the meeting report of the British Association for the Advancement of Science on which it was based was signed by, among others, Charles Darwin and Richard Owen (see Rookmaaker 2011 for more details).

[23] In so doing Stamos follows Beatty (1985) who held that Darwin wrote about species as if they were merely nominal but actually thought they were real to get his evolutionary message across. Stamos (2007, e.g. p. xi) rejects this view that he calls the received view on the topic, and instead offers a new strategy theory.

descent "trumps all others—including one based on similarity" (see Darwin 1995, p. 424, quoted at the end of Sect. 2.2). Stamos of course knows and even emphasizes this: "Instead of interbreeding as a criterion, he [Darwin] stressed common descent. In other words, his *real* species concept had a definite monophyletic [but not in the strict Hennigian sense] component to it" (Stamos 2003, p. 57). Stamos thinks that while interspecific sterility is not constitutive of species to Darwin, he (Darwin) nevertheless considers it as preliminary evidence of species distinctness, based on the fact that sterility is almost universal between species (Stamos 2003, p. 69) such that interspecific fertility is the exception that proves the rule. Stamos also cites Darwin's conclusion from the *Origin* on the species status of the *interfertile* European and Indian cattle—because Darwin assumes an independent origin of the two breeds he considers them to be two distinct species that have secondarily become interfertile after domestication (Darwin 1995, p. 254). This is in contrast to his reconstructed Darwinian species concept (see above) where the primary mark of species is distinctness in adaptive characters and descent is only secondary. This is hardly reconcilable with a primarily horizontal view of species, and it therefore seems that to Darwin the vertical dimension of species—contrary to Stamos' claims—was superior to the horizontal one.

Secondly, as he himself admits (Stamos 2007, p. 169), Stamos's theory critically hinges on his being right on how Darwin's contemporaries thought about species and varieties. Richards (2010, p. 86) writes that the strategy theory would make sense if Darwin had been facing a widespread species essentialism, but that was probably not the case. We have already seen that Darwin did not have to confront property essentialism but was rather facing a variety of ideas about species. Wilkins (2009a, p. 127) summarizes the early-nineteenth-century view like this: "It appears that while many naturalists were fixists, the leading criterion for species identification or explanation was derived from the descent of similar forms. Apart from Agassiz, nobody seems, however, to have inferred from fixism, or the pious creationism that was the usual form of words used, that species had essences or even that variation was firmly limited". And again (ibidem, p. 132): "The standard view of species at the time, since the original definition by Linnaeus, was that any two organisms were of the same species if they shared ancestry (in Linnaeus's pious formulation, from the pair of creatures created by God)". If this is true, however, Darwin's historical role as the "hero" who eliminated the prevailing Platonic idealism and introduced population thinking is at least doubtful.[24] But then, what was Darwin's historical impact on the species problem? Wilkins (2009b, p. 77) answers this question as follows: "Charles Darwin is important not so much for the novelties on the nature of the species concept that he provided—there are only

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[24] Darwin's overall importance as the one who ultimately founded evolutionary biology and, together with Alfred Russell Wallace, introduced a scientific explanation for adaptation (natural selection), which arguably was a precondition to turn biology into a full-fledged science, is not diminished by the fact that the Essentialism Story is very probably wrong. Neither is his outstanding philosophical importance beyond biology and science for the way we see the world and ourselves in it. In this regard, he has few (if any) equals.

really two of these, failure to breed in nature, and selection as the motive force of specific characters. Rather it is because his book *On the Origin of Species* changed *every* scientist's way of looking at species thereafter". It is not so much a particular species concept by which Darwin has impacted on the species problem, but rather a "paradigm shift" (Kuhn 1962). Indeed, biology after Darwin was not the same. Evolution offered new insights and explanations and in this sense revolutionized biology (as encapsulated by Dobzhansky's (1973) famous dictum that "Nothing in biology makes sense except in the light of evolution"). However, in many practical ways, this theoretical earthquake had surprisingly little impact, and that is certainly true for taxonomy. To this day the pre-evolutionary Linnaean system of classification is in use (however often this has been bemoaned), and while taxonomists certainly work within an evolutionary framework in theory, the very practice of describing and naming species is often decoupled from such theoretical underpinning. This is not true for phylogenetic analyses in taxonomy, of course, but a description of the morphology of an organism and how distinct it is from related taxa and the conclusion that it is a distinct species is operationally the same in an evolutionary and a pre-evolutionary context. Darwin was well aware of this when he wrote "When the views entertained in this volume on the origin of species, or when analogous views are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history", only to start the directly following sentence with "Systematists will be able to pursue their labours as at present" (Darwin 1995, p. 424). Endersby (2009) shows, based on an analysis of Joseph Hooker's botanical work, that "For all practical purposes, there was no difference between post- and pre-Darwinian taxonomy" (p. 1498), and he goes on to conclude: "A scientific revolution that makes no difference to everyday scientific work seems an odd sort of revolution, yet it was precisely this conservatism that helped make Darwin's version of evolution acceptable to naturalists who had rejected earlier theories" (p. 1499).[25]

2.4 From Darwin to the Modern Synthesis

I will limit the post-Darwinian summary to the time up to the Modern Synthesis[26] because that is by and large when the present debates start. Many of the issues and concepts discussed, championed or introduced by the architects of the Synthetic

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[25] There is an analogy from politics: democratic and non- or even antidemocratic political systems can be viewed as different political and ideological paradigms, yet when there is a change from one to another—through a coup or a revolution, for example—administration often goes on as before, despite fundamental changes on a higher or more fundamental level.

[26] The Modern Synthesis (ca. 1920–1950) resulted in the so-called Synthetic Theory of Evolution and is the reconciliation of Darwinian selection with genetics and the rejection of alternative theories like Neo-Lamarckism, orthogenesis and saltationism (see Mayr and Provine 1980, Chap. 11 in Bowler 1989, Junker and Engels 1999 and references therein).

Theory are still being discussed today. More details on this period can be found in the two exquisite books by Wilkins (2009a, b) on which I have again, directly or indirectly, drawn a lot.

According to the last paragraph of the preceding section, Darwin's influence on species notions was more in the realm of the overarching philosophical framework rather than in biological practice. While this distinction is important, it is of course obvious that talking about species was not the same after the acceptance of evolution as a historical fact. Among biologists, it took about until the end of the nineteenth century for evolution to be widely accepted. Ironically, the fact that species were now entirely confined to the scientific realm sometimes meant that their reality was questioned—not in spite of but *because* of evolution. In a creationist paradigm, species are real because they are the separate units of the Creation itself, but in an evolutionary paradigm, this discreteness dissolves into a continuous stream of parent–offspring relations with vague boundaries—the very reason why species delimitation has remained difficult and contentious even more than 150 years after the *Origin*.

Among Darwin's famous contemporaries and evolutionary allies the view of Alfred Russell Wallace, the co-founder of the law of natural selection, may be of particular interest. Wallace's view on species is similar to Darwin's; he, too, emphasizes adaptation and descent and regards interbreeding or the lack of it as a potential criterion for species identification. According to him we "look upon a species, not as a distinct entity due to special creation, but as an assemblage of individuals which have become somewhat modified in structure, form, and constitution, so as to adapt them to slightly different conditions of life; which can be differentiated from allied assemblages; which reproduce their like, and which usually breed together—we require a fresh set of experiments calculated to determine the matter of fact,—whether such species crossed with their near allies do always produce offspring which are more or less sterile *inter se*" (Wallace 1912, p. 167). And again: "Species are merely those strongly marked races or local forms which when in contact do not intermix, and when inhabiting distinct areas are generally believed to have had a separate origin, and to be incapable of producing a fertile hybrid offspring (...) we have no means whatever of distinguishing so-called 'true species' form the several modes of variation here pointed out, and into which they so often pass by an insensible gradation" (Wallace 1870, p. 161, quoted in Wilkins 2009a, p. 161). This is again a generative notion *sensu* Wilkins, and it also emphasizes the problem of fuzzy boundaries, making the species level as a category difficult to grasp.

Asa Gray also embraces the generative notion, and very explicitly so: "Objectively, a species is the totality of beings which have come from one stock, in virtue of that most general fact that likeness is transmitted from parent to progeny. (...) The two elements of species are: (1) community of origin; and, (2) similarity of the component individuals. (...) It is from the likeness that the naturalist ordinarily decides that such and such individuals belong to one species. Still the likeness is a consequence of the genetic relationship; so that the latter is the real foundation of species" (Gray 1879, p. 317f, quoted in Wilkins 2009b, p. 98f.). This quotation is interesting because it encapsulates a common taxonomical problem that we still face today: similarity (often demonized as a sign of essentialism or typology) is an important guide to the underlying historical relationships. Ultimately, it is the *only* such guide[27] and thus has to come into play sooner or later operationally when species are delimited (see Chap. 6).

Thomas Henry Huxley, according to Wilkins (2009a, p. 166), seems to have been well aware of the difference between the T species of taxonomic practice and theoretical notions about species: "the smallest groups of animals which can be defined one from the other by constant characters, which are not sexual; and these are what naturalists call SPECIES in practice, whatever they may do in theory" (Huxley 1906, p. 226f., quoted in Wilkins 2009b, p. 111). He also distinguishes morphologically delimited species from physiological species which are based on interbreeding: "Living beings, whether animals or plants, are divisible into multitudes of distinctly defineable kinds, which are morphological species. They are also divisible into groups of individuals, which breed freely together, tending to reproduce their like, and are physiological species" (in a review on Darwin's *Origin of Species*, see Huxley 1893, p. 50[28]).

There are also nominalist positions among the early post-Darwinian evolutionists of the late nineteenth and early twentieth century. Charles E. Bessey, a botanist and student of Asa Gray's, is a typical example of those who deny species on the grounds of the continuous evolutionary process: "Nature produces only individuals, and nothing more. (. . .) So species have no actual existence in nature. They are mental concepts, and nothing more. They are conceived in order to save ourselves the labor of thinking in terms of individuals, and they must be so framed that they do save us labor. If they do not, they fail of their purpose" (Bessey 1908, p. 218f.). So, to Bessey species are always and only taxonomic T species. He also advocates a compromise between lumping and splitting (to "steer a course between these two extremes", p. 219), precisely because species are only conveniences to him. Evolution has rendered the species category void: "As long as species were supposed to be actual things, 'created as separate kinds at the beginning,' that botanists 'discovered', as explorers discover islands in the ocean, there was no serious 'species question'" (p. 218).

The early geneticists (Thomas Hunt Morgan, Hermann Joseph Muller and John B. S. Haldane) usually held views similar to that of Bessey in that they tended to deny the reality of species and to regard the concept as one of convenience or taxonomic necessity (Wilkins 2009b, p. 123, 129, 130). In *Evolution and*

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[27] Similarity is not identical to phenetic overall similarity. Apomorphies are also a kind of similarity, so this is true also for cladistic approaches. Similarity is particularly important when it comes to delimiting species horizontally, i.e. agreeing on how inclusive species-level lineages should be.

[28] I owe this quote to Wilkins (2009a, p. 166). According to my copy of Huxley (1893), however, this review was published in 1860, not in 1859, and this is in accordance with other sources (e.g. information on http://darwin-online.org.uk according to which the review was published as "Darwin on the origin of Species" in Westminster Review 17 (n.s.), pp. 541–570 in 1860).

Adaptation from 1903 (p. 33), Morgan says: “We should always keep in mind the fact that the individual is the only reality with which we have to deal, and that the arrangement of these into species, genera, families, etc., is only a scheme invented by man for purposes of classification. Thus there is no such thing in nature as a species, except as a concept of a group of forms more or less alike. In nature there are no genera, families, orders, etc. These are inventions of man for purposes of classification”. And Haldane holds: “I object to the term ‘species concept’, which I think is misleading. (...) A species in my opinion is a name given to a group of organisms for convenience, and indeed of necessity” (Haldane 1956, p. 95, quoted in Wilkins 2009b, p. 130).

Hugo de Vries, a botanist and early geneticist who is famous for his saltationist notions on evolution, only partly agrees with such views. To him, there are two sorts of species which correspond to T and E species. The former he calls systematic species, the latter elementary species: “we must recognize two sorts of species. The systematic species are the practical units of the systematists and florists, and all friends of wild nature should do their utmost to preserve them as Linnaeus has proposed them. These units, however, are not really existing entities; they have as little claim to be regarded as such as genera and families. The real units are elementary species” (de Vries 1905, p. 12). Elementary species are pure genetic lines, and systematic species usually comprise a number of them. Systematic species as artificial groups of several elementary species are important in order to make classifications practical because the acceptance of elementary species only would multiply the number of species. While acknowledging the difference between T and E species, to de Vries T species are never meant to approach reality as hypotheses of E species; rather, they are mere conveniences.

Ernst Haeckel, the famous German evolutionist and monist, criticized discussions on whether a group of organisms should be classified as species, subspecies or varieties as void: “Endless disputes arose among the ‘pure systematizers’ on the empty question, whether the form called a species was ‘a good or bad species, a species or a variety, a sub-species or a group’, without the question being even put as to what these terms really contained and comprised. If they had earnestly endeavoured to gain a clear conception of the terms, they would long ago have perceived that they have no absolute meaning, but are merely stages in the classification, or systematic categories, and of relative importance only” (Haeckel 1886, p. 115). This at least shows that, perhaps like Darwin, Haeckel thinks (and from his further discussion it becomes clear that the continuousness of the evolutionary process is the underlying reason) that there is no non-arbitrary demarcation between species, subspecies and varieties. According to Wilkins (2009b, p. 110), Haeckel’s views on species are rather typical of his time.

Starting with the turn of the century, we find more and more notions of species that are still with us today. Darwin’s friend and research assistant during his last years George Romanes, for instance, gives a list of all (to him at least) logically possible definitions of species, and this list includes something very close to the Biological Species Concept and various versions of a concept that is basically identical to the diagnosability version of the Phylogenetic Species Concept (see

Chap. 4), the closest of which is “A group of individuals which, however many characters they share with other individuals, agree in presenting one or more characters of a peculiar and hereditary kind, with some degree of distinctness” (Romanes 1906 [1895], p. 231).

Arguably the most important and influential publication around the turn of the century was *What is a species?* by Edward B. Poulton (1904). To Wilkins (2009b, p. 112) this essay “marks the beginning of the debate of the present day” (see also Mallet 2004a, b for an appraisal). In it, Poulton (who had a knack for coining terms derived from Greek) defined syngamy as the free interbreeding under natural conditions and synepigonic forms as those descended from a common ancestor. A species to him, then, was “a syngamic and synepigonic group of individuals, an objective reality however difficult to establish in practice”; and “[u]nlike and apart from genera, families and other groups employed in our ‘little systems’ of classification which ‘have their day and cease to be’, not only do individuals stand out as objective realities, but equally real, though far less evident, are the societies into which individuals are bound together in space and time by Syngamy and Epigony” (quoted from Wilkins 2009b, p. 113f.). From this it becomes clear that to Poulton a species’ ontological reality is independent of operational difficulties in identifying it, a view that is still widely held today. Poulton points out that for asexual taxa one has to rely on genealogy (epigony) alone, implying that he does accept asexual species. He is also very aware of the practical difficulties of species delimitation caused by fuzzy boundaries and the ensuing arbitrariness in taxonomy: “transitions are infinite in their variety; while the subjective element is obviously dominant in the selection of gaps just wide enough to constitute interspecific breaks, just narrow enough to fuse the species separated by some other writer, dominant also in the choice of the specific characters themselves” (ibidem p. 114).

Poulton’s views and his emphasis on interbreeding under natural conditions, along with similar views held by Karl Jordan,[29] had a strong influence on Ernst Mayr and “his” Biological Species Concept (Mallet 2004a). Wilkins (2009a, p. 173f.) summarizes the importance of Poulton’s essay like this: “Prior to Bateson’s and Poulton’s essays, there was no species *problem* as such but only a species *question*. The latter is concerned primarily with the origins of species, how they come to be. The *problem* arises when we have accounts of species formations, whether by selection or something else, that do not involve immediate saltation from one to another or *creatio de novo*. It is the problem of defining what rank it might be that species achieve when they become species, and this sets the agenda for (. . .) the remainder of the twentieth-century debates”. The reference to Bateson is because in his 1894 book, he emphasized the difficulty of “defining species under the theory of transmutation of species” (Wilkins 2009b, p. 117). While the “species problem” as understood here (i.e. defining the species rank) is much more narrowly

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[29] See Jordan (1905). Mallet (2004a) points out that Mayr and Jordan had both worked at Tring for the collection of Walter Rothschild, and thus the influence of the much older Jordan seems obvious.

defined as in Sect. 1.1, it still becomes clear that particularly Poulton's paper was a milestone for the modern debate.

Around the time of the beginning of the Modern Synthesis, there were also pluralist positions with regard to species. The Swedish botanist Görte Turesson, for example, called it a "logical impossibility to reach one standard definition of the 'species'" (Turesson 1929, p. 332). This and an awareness of the difference between T and E species led him to distinguish between different kinds of species (Turesson 1922a, b, 1929) that vary in their inclusiveness (e.g. his coenospecies comprise various ecospecies), but he emphasizes interfertility in sexual species and common descent in general. He also distinguishes between species in sexual and asexual taxa and uses the term agamospecies (based on common descent) for the latter.

The difference between sexual and asexual taxa was also highlighted by Ronald A. Fisher, one of the founders of mathematical population genetics and thus an early and very important figure in the Modern Synthesis. In his groundbreaking *The Genetical Theory of Natural Selection* from 1930, he says about completely asexual taxa (the existence of which he still doubted at the time, Wilkins 2009a, p. 182): "Species, properly speaking, we could scarcely expect to find, for each individual genotype would have an equal right to be regarded as specifically distinct, and no natural groups would exist bound together like species by a constant interchange of their germ-plasm. The groups most nearly corresponding to species would be those adapted to fill so similar a place in nature that any one individual could replace another, or more explicitly that an evolutionary improvement in any one individual threatens the existence of the descendants of all the others" (Fisher 1930, p. 121). This quote is interesting and has been chosen because it points at a number of issues linking it to the present debate: (1) it includes clear differences between sexual and asexual species and denies that the latter, strictly speaking, exist; (2) gene flow ("interchange of germ-plasm") and thus also interfertility play an important role in sexual species; (3) there are criteria that we can find in very specific modern species concepts: the capacity of conspecific individuals to replace one another in their place in nature is clearly reminiscent of what Templeton would later call demographic exchangeability in his Cohesion Species Concept, and the second part (that an evolutionary improvement in one individual threatens the existence of the descendants of all others) is similar to Ghiselin's Reproductive Competition Species Concept (see Chap. 4 for details on Templeton's and Ghiselin's concepts). All of these issues will be taken up again in the following chapters.

Chapter 3
The Metaphysics, or Ontology, of Species: Classes, Natural Kinds or Individuals?

3.1 Classes, Natural Kinds, Sets and Individuals

I have already stated that the species problem is in large parts a philosophical rather than a biological issue. For no other part of the problem is this as true as for the question of the ontological status of species, i.e. the question “what kind of things” species taxa are. The usual suspects for the answer to this are classes, natural kinds (which are a special kind of classes) or individuals, with some quite sophisticated variations and hybrids of these three. Few other issues have produced so much literature as this one when it comes to species, and a whole new book could be written about the ontology of species and the new arguments since the publication of Ghiselin (1997)—but it would not be a book for biologists. I will only give a brief summary of the main lines of thought. This is sufficient for two reasons: (1) it is in line with the general aim of this book, and (2) it is my personal conviction that the issue is really not as difficult as it might seem—at least as far as its relevance to biologists is concerned. This is not to say that the ever more sophisticated contributions to the debate are idle. In fact, they are often very interesting from a philosophical point of view—and they often transcend the issue of biological species to much more general problems about kinds and entities. But it is probably fair to say that for biologists in general and even for taxonomists and evolutionary biologists, the more remote ramifications of the “classes/kinds vs individuals” debate hold little to gain. Readers interested in professional discussions of the debate are referred to Chap. 6 in Richards (2010) as an introduction and then perhaps to the relevant chapters (3–5) in Stamos (2003). These two also contain the most relevant references except for very recent ones. And then, there is of course the “bible” of the individuality thesis, Ghiselin’s important book from 1997. It is much less neutral of course but a gripping read.

Put very simply, species for a long time were viewed as what philosophers call classes, often as a particular type of class called natural kind. Then, in 1966 and 1974(a), Michael Ghiselin advanced what he called “a radical solution to the

F.E. Zachos, *Species Concepts in Biology*, DOI 10.1007/978-3-319-44966-1_3

species problem"—namely, that species are not classes but logical individuals, a view that he detailedly elaborated in his 1997 book *Metaphysics and the Origin of Species*. In more recent years, species were then, inspired by Ludwig Wittgenstein's concept of family resemblance, also characterized as cluster kinds or cluster classes. The vast majority of biologists dealing with theoretical questions of the species problem today consider species to be individuals, and the same holds true for a large number of philosophers of science (although among these one still finds proponents of the natural kinds/classes view). While appreciating that some of the cluster kind approaches are appealing, my own view (shared by probably the huge majority of biologists) is that Ghiselin was right, that his contribution marks a conceptual breakthrough for the philosophy of biology and evolutionary biology and that everything that has come after him may modify and improve his insights but cannot overturn them—for the simple reason that only species as individuals are compatible with evolution as a historical fact and process.

So, what, in a nutshell, are the conceptual contenders when it comes to the question what species taxa are? *Classes* are groups of particular objects and are defined by essential properties. Essential properties are both necessary and sufficient, meaning that all members of the class exhibit these properties and that all objects exhibiting these properties are members of the class. These particular objects are often called elements of the class and are said to instantiate the class or to be instances of the class. For example, the class of red triangles contains all red triangles in the universe (and beyond), and every red two-dimensional figure with three straight sides and three angles is an element of that class. Importantly, classes are not spatiotemporally restricted: they are independent of time and space! While elements or instances may come and go, the class remains the same. Even if there is not a single red triangle in the world, the class of red triangles is still there (but empty). Classes are eternal and exist at all times and places. Whether such classes really exist outside our minds is contentious. As briefly mentioned in Sect. 1.5, the argument over the reality of universals (does "redness" exist, or do only particular red things exist?) has a long history. The view that universals exist independently of their instances is usually called realism, while the opposite view that only particulars really exist is called nominalism. However, this dichotomy is perhaps a little too imprecise as often a further view is distinguished: conceptualism. Under this trichotomy, nominalism holds that only particulars exist (and universals are merely words or vocal utterances), conceptualism denotes the view that universals do exist but are dependent on the human mind (i.e. are concepts in our mind), and realism grants to universals existence independently of the human mind (Audi 2009, p. 752; see also p. 169 and 563; Richards 2010, p. 114, Stamos 2003, p. 8f.). For biologists pondering the ontology of species, it is probably most important to note that whether or not universals/classes exist in a philosophical sense, any such existence will be different from the existence of particular historical objects (see below when individuals are discussed).

Natural Kinds are a specific type of class and in many regards the most important and most interesting one or, as Hull (1992, p. 183) puts it, "privileged classes". Like classes natural kinds have essences (necessary and sufficient properties), but they are often granted extramental reality which is why they are called "natural": "To say that a kind is natural is to say that it corresponds to a grouping that reflects the structure of the natural world rather than the interests and actions of human beings [. . .] The existence of these real and independent kinds of things is held to justify our scientific inferences and practices" (Bird and Tobin 2015). The standard examples of natural kinds are chemical elements and chemical compounds: any and every atom and only those that have an atomic number of 79, i.e. that have 79 protons in their nucleus, are instances of the natural kind gold, and any and every compound particle H_2O (and only those) is an instance of water. In that regard, natural kinds are not different from the class of red triangles or of all cars manufactured in Germany, but there are intuitive differences as Bird and Tobin (2015) put it: "Intuitively, to group all instances of the metal zinc together is to engage in a natural classification, whereas to group together Trajan's column, the number two, and Julius Caesar is to classify things in an arbitrary manner. The classifications 'cars manufactured in Germany', 'culinary vegetables', 'altars' are not arbitrary, but neither are they natural, since they reflect human interests".[1] What sets natural kinds like chemical elements apart from classes like cars manufactured in Germany is that their grouping is based on natural causes or laws and that the discovery of these natural kinds therefore represents an increase in our knowledge on the structure of the world. This short depiction is very superficial; the topic goes much deeper and touches on basic metaphysical questions of philosophy, but these are the scope of evolutionary biology. What is important to note is that when species are viewed as classes with essential properties, this does not necessarily entail that they are unnatural and completely arbitrary groupings.

Another related term that is similar to that of classes is *set*. Some distinguish between classes and sets, and some treat these terms synonymously (see Stamos 2003, pp. 20–21). When a distinction is made between the two, classes are usually defined intensionally, while sets are defined extensionally. An intensional definition is one based on the specification of the necessary and sufficient (i.e. essential) properties of a group; an extensional definition is simply giving a list of all members of a group (the group named above containing Trajan's column, the number two and Julius Caesar is an example). For the scope of this book, this distinction is largely irrelevant, and therefore I will speak of classes and mean by them all groups defined by essential properties.

The ontological alternative to spatiotemporally unrestricted and/or arbitrary or artificial entities is to view species as *individuals*. The term itself is perhaps not the best choice because intuitively we think of individual organisms when we hear individual, which makes it somewhat ambiguous. However, individuals may be more widely defined as spatiotemporally restricted historical entities. The Roman

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[1] To be precise, this view is only one of the several possibilities and holds that natural kind classifications are really natural and have extramental reality (naturalism or realism). One can of course also deny their reality (and, for that matter, the reality of basically everything).

Empire, the acting company The King's Men and the Habsburg dynasty are individuals in this sense—they are historical entities that have a beginning and an end in time. Once an individual dies or ceases to exist, it can never exist again. A new empire can rise to power in the Mediterranean with Rome as its capital (and perhaps even with emperors, a senate and consuls), but it will still be different from the Roman Empire that our history books tell us about. Unlike classes and natural kinds that have instances or elements, the relationship between an individual and its members is that of whole and parts: Roman citizens were not instances of the Roman Empire but parts thereof, just like Shakespeare was a part of The King's Men and emperor Franz Joseph I. of Austria was a part of the Habsburg dynasty. To make the difference between classes and individuals more visible, Ghiselin (1997, p. 40) has suggested to reserve the terms inclusion and inclusive for class–element relationships and to use incorporation and incorporative for whole-part relationships of individuals instead. Thus, Chordata would be a more incorporative (rather than a more inclusive) taxon than Vertebrata, but although linguistic consistency is doubtless an advantage, this distinction has never caught on. I will therefore stick to the less accurate but more common term inclusive.

Being historically contingent entities, individuals do not have essential properties—there is no necessary and sufficient condition to be the Roman Empire. This is what is really revolutionary about the "species-as-individuals" view—if species are individuals, they cannot be defined based on properties, let alone essential ones! Ghiselin (1997, p. 45) neatly sums this up: "what is necessarily true of natural kinds is true of physical necessity, whereas what is necessarily true of artificial kinds is true of logical necessity, and what is true of individuals is true only as a matter of contingent fact, and therefore not necessary at all".

But not only can species not be defined in terms of properties, they cannot really be defined at all! Rather, they can only be pointed out ostensively: "this group of organisms is *Homo sapiens*". Although really an act of christening rather than a definition, this is often called ostensive definition. Names of individuals, including species, are therefore *proper names*![2] Indeed it was this insight (that species have *proper* names) that made Ghiselin realize that species are individuals, while David Hull, the most prominent adherent of the individuality thesis among philosophers of science (e.g. Hull 1976, 1978), arrived there as a consequence of the fact that there are no laws of nature for individual species (Ghiselin 1997, p. 130). While Ghiselin's name is usually associated with the individuality thesis, there are others who have viewed species and more generally biological taxa as individuals rather than classes (which Ghiselin readily admits). Wilkins (2009b, p. 173) names W. Stanley Jevons who, as early as 1873, noted that classes must have definienda common to all its members but that biological classification is not really a classification in this sense, but rather an arrangement of groups by genealogy which are

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[2] But see Jensen (2011) who recognizes the similarity of species names to proper names but thinks that there are also differences, which is why he calls species names "extra-proper names". I will not go into further detail here of this largely philosophical discussion.

individuals in the light of evolution. To Stamos (2003, p. 186) I owe another early source of the notion that species are individuals: the very young Julian Huxley mentions "the species-individuality of which we are the parts" (Huxley 1912, p. 24), and he also seems to think that in the light of evolution, species must have individuality. Willi Hennig (1966, p. 81, drawing on the philosopher Nicolai Hartmann) was also very clear about this when he said that biological taxa are not timeless abstractions but that "there can be no doubt that all the supra-individual categories, from the species to the highest category rank, have individuality and reality. They are all [. . .] segments of the temporal stream of successive 'interbreeding populations'. As such they have a beginning and an end in time". Similar, implicit or explicit, references to the individuality of biological taxa can be found throughout the evolutionary and phylogenetic literature.[3] The reason for this is quite simple: species as timeless abstractions (classes or natural kinds) are hard to reconcile with the historical process of evolution. How could the physical and historical process of evolution produce eternal and timeless entities?! To accept this would make biological classification an artificial enterprise dealing with mere intellectual abstractions rather than real groups: "For species to evolve, it is metaphysically necessary for them to be individuals, and an 'evolutionary' species definition that treated them as if they were sets [classes] would be a contradiction in terms, or an oxymoron at the very best" (Ghiselin 1997, p. 113).[4]

It is very important to realize that the "class/kind vs individual" debate refers to the ontological status of species *taxa*! It asks what kind of thing a species taxon like *Homo sapiens* or a tiger is. The issue of what the species *category* is (i.e. the group of all species taxa) is an entirely different question, and except for species category nominalists (who deny that something like the species rank exists), everyone agrees that the species category is a class with all species taxa as its members or elements. What exactly defines this class—what its necessary and sufficient properties are—is the vexed issue of which species concept is the best, but everyone who favours a certain species concept has already agreed that the species category is a class.

The individuality thesis does not stop at the species level. It includes all higher taxa as well inasmuch as they correctly represent history, i.e. phylogeny. Monophyletic supraspecific taxa are also individuals: they originate in the form of their stem species, and at some point, they become extinct (or still exist today). Just like species, higher monophyletic taxa cannot be defined by properties either. They can only be pointed out in the Tree of Life, and nested parts of this tree that fulfil the conditions of monophyly are given a name (ostensive definition), which is a proper name. The properties that are unique to this taxon (its autapomorphies) must not be

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[3] For the German-speaking world, Rieppel (2011) traces the view of species as individuals back to pre-evolutionary times when the German *Naturphilosophie* as developed by Friedrich Schelling assigned individuality to species due to their passing through time (spatiotemporal restrictedness).

[4] Stamos (2003, p. 287, footnote 4) presents an interesting quote from Bertrand Russell in regard to Darwin's *Origin of Species*: "The doctrine of natural kinds [. . .] was suddenly swept away forever out of the biological world" (Russell 1914, p. 22). Russell, however, seems to have held different views on the ontology of species at different times and was overall not very interested in the topic.

confused with its definition—they only serve to *discover*, not to define the monophylum!

3.2 Whatever else Species Might Be, They Must also Be Individuals

As mentioned before, the term "individual", looking back on the debate, may not have been the best choice. I would agree with Ghiselin that it is an appropriate term for an entity that is spatiotemporally bounded, but there are stricter definitions of individuals, stipulating, for example, that in addition to spatiotemporal restriction, an entity is only an individual if its parts are interconnected. In the case of species, this interconnection would be some kind of cohesion among the single conspecific organisms. Usually species are compared to organisms, the prime examples of individuals, and the discussion is about whether species show the same kind and degree of integration and cohesion as single organisms (e.g. through gene flow or exposure to similar selection regimes) and, if they don't, whether they should be called individuals. Accordingly, there have been futile arguments over the use of the term rather than the important issues that stand behind it—quite apart from the fact that even the autonomy and concreteness of organisms is a matter of degree with sometimes vague boundaries (think of slime moulds or colonial organisms). One has to be careful here that one does not just have a purely terminological debate. Wiley (1980, 1981, p. 74f.) has made an interesting (but terminological) point by introducing the term "historical entity" or "historical group". Of course every individual is a historical entity, too, but Wiley wants to make a distinction between two different kinds of historical entities: those that show cohesion among its parts and partake (at least potentially) in natural processes, and those that don't. The first Wiley calls individuals (and he includes species here), the second he calls historical entities or groups. His definition thus subdivides further what is called individual by others (e.g. Ghiselin or Hull), and Wiley (1981, footnote on p. 75) admits that this distinction is primarily interesting from a philosophical rather than from a biological perspective. While, according to Wiley, species are individuals in the narrow sense, higher monophyletic taxa are not because, unlike species, they lack cohesion and do not partake in natural processes (Wiley 1980, 1981, p. 75). This distinction, I think, is correct, but whether it grants a new term (and one that is rather vague) is a different matter. I will use the term "individual" in a general sense, i.e. as a term for historical (= spatiotemporally restricted) entities. Everything that has a beginning and an end in space and time is an individual under this definition, an individual sensu lato, as it were. What is important is that both individuals sensu lato and individuals sensu stricto are clearly very different from their ontological alternative: classes or natural kinds. If biologists or philosophers deny individual status to species, it must therefore always be asked whether this is because of a stricter definition of the term individual or because they consider species to be classes/natural kinds. The former is primarily an issue of nomenclature, while only the latter is a true ontological or metaphysical issue. I have chosen to use the sensu lato definition of individual not because I think it is a good application of the term (although I do think it is) but mainly for historical reasons: it is the conception of individuals held by Michael Ghiselin who is the father of (at least the explicit) treatment of species as individuals (Ghiselin 1966, 1969, 1974a[5]). Therefore, I think that it is historically consistent to use and evaluate the term in its original contextual meaning. Whether Wiley is correct in classifying species as individuals sensu stricto and whether higher monophyletic taxa are really different from species in that regard is a valid and interesting question, but it is one that is asked already within the paradigm of species as spatiotemporally bounded entities, which precludes their being viewed as natural kinds. Or as Ghiselin (1997, p. 59) puts it: "cohesion or the lack of it does not seem to imply a deep metaphysical cut [. . .] The difference between historical entities and cohesive individuals may be important, but it is far less profound than that between historical entities and classes". This view is shared by Baum (1998, p. 643) who treats entities with a common history that lack causal interactions as "simply one type of individual (broad sense)". Ghiselin (1997, p. 52) concludes that cohesiveness is sufficient but not necessary for individuality, and it is also sometimes temporary in organisms, giving slime moulds ("social amoebae") as an example (p. 55). This example is revealing because it shows that the term organism is by no means as clear-cut as many philosophers, who mainly think of large vertebrates when they think of organisms, would like it to be (Richards 2010, p. 163f.). Accordingly, cohesiveness is not included in Ghiselin's list of "six criteria by virtue of which individuals may be recognized and individuality may be defined: 1. non-instantiability[[6]], 2. spatio-temporal restriction, 3. concreteness, 4. not functioning in laws, 5. lack of defining properties, and 6. ontological autonomy" (ibidem, p. 49). Mishler and Brandon (1987) give a slightly different but similar list: spatial boundedness, temporal boundedness, integration and cohesion. The difference between the latter two is that cohesion (in their terminology) implies that an entity "behaves as a whole with respect to some process", whereas integration refers to "active interaction among parts of an entity. In other words, does the presence or activity of one part of an entity matter to another part?" (p. 400).

I will not discuss all these criteria in detail. This has been done in many of the publications cited here, and it is beyond the scope of the book. It is also beyond what is of immediate relevance and benefit for practicing biologists. Instead, I will

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[5] Ghiselin (1997, pp. 14ff.) gives a short summary of how he came to think of species as individuals, that his first publication with the individuality thesis was the one from 1966, that he elaborated on it in his 1969 book, but that his 1974a paper really triggered the general discussion.

[6] Non-instantiability refers to the fact that there are no instances of individuals as there are instances of classes: while all concrete circles are instances of the abstract class of circles (by meeting the essential condition(s) of class membership), individuals do not have such instances or elements. Instead, they have parts, and just like my left arm is a part of me and not an instance or element, Greece and France are parts of the European Union, not their instances.

highlight some aspects and then discuss some arguments why species should not be viewed as individuals. The issue of cohesion will be taken up again in Chap. 6 when species delimitation is discussed in more detail. As for concreteness, it should be kept in mind that this is largely an issue of scale and perspective. If species have boundaries in space and time (and how could they not if they are products of the historical process of evolution?), then that entails some level of concreteness—however, one far beyond the limited scope of human perception. To an external observer that lived for millions of years, species will appear much more concrete than to us, and the same applies to the spatial dimension: an individual organism or a piece of rock to us seems to have well-defined boundaries, but when zooming in on the micro- and nano-level, these boundaries become fuzzier and fuzzier.

With regard to the individuality of species, two points have been raised repeatedly: punctuated equilibria and species selection. Punctuated equilibria (Eldredge and Gould 1972) indeed supports the notion of individuality because the pattern it proposes—evolutionary change at the beginning of a species' life time followed by stasis—makes the spatiotemporal joints at which we are to cut up nature more pronounced. In his *opus magnum*, Stephen Jay Gould (2002, p. 776) sums this up (overly simplistically, one might add) like this: "Thus, the classic and endlessly fretted 'species problem in paleontology' disappears because species act as well-defined Darwinian individuals, not as arbitrary subdivisions of a continuum". These species boundaries (beginning and end in time and space), however, must exist regardless of whether the theory of punctuated equilibria is an accurate description of speciation and the fossil record, and therefore the question of individuality is independent of the debate of punctuated equilibria (Stamos 2003, p. 220ff. provides a detailed discussion).

If species are individuals, then it is possible for them to partake in processes. The possibility of species selection (Stanley 1975, 1979)—i.e. selection operating not only on the level of the individual but also among species as a whole (via differential rates of survival against extinction and differential rates of speciation)—is therefore interesting for adherents of the individuality thesis. If species can act as the unit of selection, then that would endorse the view that they really are individuals. However, it is important to realize that species selection is only a possible, but not a necessary property of species if they are individuals. Whether there really is such a thing as species selection is an empirical issue, and while a positive answer clearly is almost conclusive evidence for individuality, a negative answer does not refute that species are individuals. In line with this, Stamos (2003, p. 211f.) calls the species selection debate a red herring in the discussion about the ontology of species, contrary to Ruse (2008, p. 136) who thinks that the demise of group selection is a serious blow to the individuality thesis.

Although, in principle, all knowledge is hypothetical and in that sense preliminary, no serious biologist or philosopher doubts that evolution is a historical fact and that species evolve. This necessarily makes them historical entities and, thus, individuals (in the broad sense of the word). To view species as classes or natural kinds seems, against this background, equivalent to claiming that the species *Homo sapiens* already "existed" two billion years ago or, more precisely (since classes are independent of space and time), has always been around, even before our universe came into being—as an empty class with no elements. This would have to be true not only for humans but for every other species as well, and that includes those that have not yet evolved. Species therefore are individuals and nothing else, or are they? Why do particularly some philosophers maintain that there must be more to species than individuality, that they are indeed natural kinds (e.g. Kripke 1972; Kitts and Kitts 1979) or that they are some kind of ontological hybrid? Some of their arguments are actually well worth pondering. One of the most famous adherents of the "species as natural kinds" thesis is Michael Ruse (e.g. Ruse 1987, 1998). He does not argue in favour of natural kinds in an Aristotelian (real essences) or Lockean (nominal essences) way but rather holds that their objective existence is due to "consilience of induction" (Whewell 1840), i.e. the fact that different species concepts coincide in combining organisms into groups (species). In this, I think, he is misguided because I do not see why the consilience among different species concepts in delimiting species entities (and that consilience really only goes so far as every taxonomist will confirm) should contain information on the ontological status of these entities. Stamos (2003, p. 93, footnote 28) also thinks this argument flawed: "what Ruse fails to recognize is that consilience can only serve to establish that 'good' species taxa are objectively real, such as *Homo sapiens* or *Gorilla gorilla*; it cannot also serve to establish the ontological status of those taxa [...] Indeed Ruse seems to confuse taxa with category. He thinks consilience can establish that species taxa are natural kinds, but this is mistaken; at most, consilience can only establish that the species *category* is a natural kind". However, Ruse does offer two interesting arguments that at least challenge the seemingly clear-cut "species-as-individuals" thesis. In his very entertaining review of Ghiselin's *Metaphysics and the Origin of Species*, "All my love is towards individuals" (Ruse 1998; the rather poetic title is a quote from a letter of Jonathan Swift to Alexander Pope), he raises two partly rhetorical questions: if *Tyrannosaurus rex* were cloned from ancient DNA, would the result be the same species as the one that became extinct some 66 million years ago? And what about independently arisen polyploids that are reproductively isolated from their parental population—aren't they the same species? While the first question is purely hypothetical and far removed from real taxonomic issues, the second problem—to which we might add the related phenomenon of repeated hybridization events among the same parental populations or species—is very real.[7] The first example, then, is about whether species extinction is necessarily forever; the second is about the independent origin of genetically (more or less) identical entities. And the question is what this means for the individuality thesis. Stamos, who holds that species are neither classes or natural kinds nor individuals but complexes of similarity relations (see Sect. 3.5 and his biosimilarity species concept in Chap. 4), holds that species can have multiple origins and that extinction is not necessarily forever because he thinks that the

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[7] Hybrid speciation, even without considering polyploidy, seems to be much more common than assumed before the genetic era (Mallet 2007).

synchronic dimension of species is superior to the diachronic dimension and because similarity relations (unlike individuals) are spatiotemporally unrestricted (Stamos 2003, e.g. p. 318, 349). Whether or not his argumentation is inherently consistent if one accepts his species definition, I don't think these examples or hypothetical scenarios are necessarily a serious blow to species individuality, although they do show that species ontology can be really tricky. First of all, one has to realize that taxonomic practice in this case may be a poor guide. Whether or not it is justified to subsume the hypothetical cloned *T. rex* under the extinct species that palaeontologists know as *Tyrannosaurus rex*, if it really were to happen, that poor creature would in all likelihood be named *Tyrannosaurus rex*, if only for the sake of convenience. This, however, means little more than that the Cretaceous and the present *T. rex* are both given the same (T, not E!) species name. The same holds for independently arisen but otherwise identical hybrids and polyploids. For practical reasons, they could be subsumed under the same name (although one could add an asterisk, use inverted commas, etc. to make clear that something is different here). This is indeed often done (see the Welsh groundsel example below), but there are also authors who refuse to allow for numerically identical but independently arisen species. Frost and Wright (1988) provide one such example (that I owe to Stamos 2003, p. 308). These authors, embracing the individuality thesis of species, deny the conspecificity of independently arisen unisexual whiptail lizards (*Cnemidophorus* sp.): "Every origin of a uniparental historical group by hybridization (or other means) from biparental ancestors constitutes the origin of a new entity and therefore a species. [...] Uniparental historical groups that do not share the same original uniparental ancestor are not and should not be considered the same or conspecific, even if they do share the same set of parental species. Regardless of similarity by *any* measure, historical groups derived from different origins [...] do not constitute one entity and should not be forced into one binomial" (Frost and Wright 1988, p. 204f). Consequently, they recommend that the nominal (= T species) *Cnemidophorus velox*, for which there is evidence of independent origin, "be referred to as the *C. velox* complex" (p. 207).

Leaving practical taxonomical issues aside, what ontological status would the resurrected *T. rex* or dodo or woolly mammoth, etc. have?[8] Would it be a different or the same species as the extinct population? I cannot offer a definitive answer, but perhaps the following line of thought might shed some light on the question: Compare the resurrected dodo to a "dodo" population that *evolved* independently on a different planet (or on earth but from a different ancestral species) but that was

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[8] The woolly mammoth has recently been a popular candidate for resurrection and cloning attempts, and the dodo is a classic example. Stamos (2003, p. 241) quotes David Hull (1988, p. 79): "*Dodo ineptus* [= *Raphus cucullatus*] is conceptually the same sort of thing as the Baroque period. Both are gone and can never return. Extinction is necessarily forever", but then objects to this by saying: "Thus a genetically engineered dodo would not be like a replica of a Tiffany lamp; it would be like a Tiffany lamp, the real thing. That it does not belong to the original period is disanalagous and irrelevant. If it looks like a dodo, if it moves like a dodo, if it has the DNA of a dodo, etc., then it's a dodo!" (Stamos 2003, p. 246).

identical in every regard, including the complete genome. I cannot help but think that ontologically the two scenarios are different. The independently evolved population would be a different individual and a different species with a completely different history. The resurrected dodo is taken from the extinct population—not materially, but the information (the DNA sequence of the dodo genome that served as a template to genetically engineer the new dodo) is copied from one of the extinct dodo specimens. If a frozen mammoth cell nucleus were transferred into an egg cell of a female elephant which then gave birth to a mammoth calf, the link would even be material. In either case, the genetic information of the real dodo or mammoth species is copied and used to create a new individual. In other words, this is a fairly conventional process: reproduction, albeit artificially enabled reproduction. Deep-freezing sperm or egg cells for later use is—from an ontological perspective—the exact same thing. We use our intellectual capacities to develop technology that bridges the time gap between the last historical dodo and the present one, but the genetic information of the living dodo would be *homologous* to that of the extinct population because homology ultimately means to go back to the same origin or ancestor or, more generally, to be derived from the same piece of original information. Genetic engineering or cloning of extinct species based on the actual genome of the extinct population could then, again from an ontological perspective, be described as human-aided dormancy or diapause. The identical genome of our "dodo" on a different planet, on the other hand, would have come into being completely independently of the dodos on earth; it would be *analogous*. Therefore, one could argue, the resurrected dodo is the same as the extinct one, while the extraterrestrial is not. The same reasoning applies to resurrected languages, another analogy often invoked. Modern Hebrew is based on sources of its ancient predecessor and as such homologous to the language of the Tanakh. There is one difficulty with this argumentation, though: what about historicist architectural styles such as Neo-Gothic or Neoclassicism? They, too, are modelled on their historical predecessors, so the stylistic information on which a neo-Gothic church from the nineteenth century is based is the same as (and thus homologous to because copied from) the stylistic information that is at the heart of Westminster Abbey or the cathedral Santa Maria del Fiore in Florence. Is Neo-Gothic then numerically the same as the Gothic period? Hull (see footnote 47) thinks it is not, but that would perhaps mean that the argument above is flawed and the resurrected dodo would have to be considered a different species (ontologically) after all. On the other hand, a church looking like a Gothic church but built in the 17th century would in all likelihood not be considered Baroque so that for an architectural style not only time but also properties are defining, whereas a tiger without stripes would still be a tiger. Of course, this analogy only goes so far, and there is more to the Gothic period than just the way cathedrals were built, all of which was different in the nineteenth century, so in this sense Neo-Gothic is not a true (intellectual) copy of the Gothic period, while the present dodo is the product of essentially the same process that was responsible for dodo reproduction in the original population: the copying of a genome. Perhaps ultimately, dealing with this question is even philosophical sophistry, and if the resurrected dodo is not a true dodo, then perhaps only in a logical way that is biologically completely irrelevant—comparable perhaps to the (logical) extinction of a stem species upon splitting into two daughter species according to the Hennigian Convention (see Sect. 5.5). There may be no satisfactory solution to this problem, but this does not diminish the fundamental insight that species are of a historical nature. But what about independently arisen hybrids and polyploids that are reproductively isolated from their parental species? Stamos (2003, p. 319f.) cites Ashton and Abbott (1992) who produced evidence for two or three independent hybrid speciation events, all in the twentieth century, from the same two parental species (*Senecio vulgaris* and *S. squalidus*) resulting in an allopolyploid new species, the Welsh groundsel (*Senecio cambrensis*), a plant from the same group as daisies. But is it a single new species? Mishler and Brandon (1987) insist that in the absence of merging (e.g. through gene flow), such units must be considered different species. They favour a monophyly version of the Phylogenetic Species Concept and only accept monophyletic taxa, including at the species level, so they argue that these hybrid populations are each monophyletic, and of course combining them into a single species would make this species polyphyletic. But even without the strict criterion of monophyly at the species level, this situation is complicated. There is probably little disagreement over how to handle independently arisen units that then exchange genetic material and become a single population. The vast majority of biologists would treat them as a single species. It would be a species with ultimately polyphyletic origins, though, which may be a thorn in the flesh of cladists, but then it could (and should) be argued that cladistics is only applicable to strictly cladogenetic systems, whereas at and around the species level, reticulation is not uncommon, precluding the strict application of cladistic methodology. There is an equivalent phenomenon to this kind of polyphyletic species in population genetics. There are two types of identical alleles: those that are identical because they are the results of replication events going back to the same original allele and those that have arisen as identical but independent de novo mutations (whether from the same or different original alleles that does not matter here). The first kind of identity is homologous and is called identity by descent (IBD); the second kind is instead homoplasious and is called identity by state (IBS). Now think of a gene pool where a number of identical alleles B arise through independent mutations (IBS alleles) from the allele A. These alleles may, through reproduction, be combined in the same individuals, and, ultimately, the population may become fixed for this allele due to natural selection or genetic drift, i.e. all individuals are homozygous for this allele. If the sister group of that population only carries the allele A, then B will be an apomorphy of the population, and of course in all subsequent generations, the trait of carrying the B allele will be considered a homology among the individuals of these generations. The merging of independently arisen entities can be dealt with relatively easily, but what if the independently arisen hybrids or polyploids do not merge but remain separate? That situation is a lot more difficult and reveals a very basic difficulty in the species debate, namely, how and if one can deal with ephemeral units in an objective and satisfactory way. We have independent entities (individuals) that do not combine into a single individual through merging, but they may still, in an extreme case, be genetically identical. Combining them into a single ontological species would make a class or set out of them, so under the individuality thesis, this is not an option, regardless of whether they receive, for practical reasons, the same T species name. Indeed, this is a counterintuitive consequence of the individuality thesis—ontologically the independently arisen groundsel hybrids are not the same species. One might try to escape this dilemma by saying one should treat them as *potentially* the same species-potentially because they might merge, but what if one of the hybrid populations becomes extinct before they merge? Permanent splits have been suggested as the mark of what makes a species (Kornet 1993), and extinction is as close to being permanent as it gets. Ironically, the very fact that the hybrid population was ephemeral and evolutionarily without consequences, as it were, would make it meet the criteria for being a valid species. This is indeed an uncomfortable corollary of the individuality thesis, and it is cases like this that are the reason why basically every biologist refrains from formally granting species status to ephemeral or temporary units, from which it follows that (1) species status can only be assigned in hindsight and (2) that some qualitative judgment of significance is indispensable (e.g. Sober 1984; Kornet 1993; O'Hara 1993; Mishler and Theriot 2000b; Sites and Marshall, 2004; see also Chap. 6). The examples discussed here may be extreme but not necessarily unrealistic (independent hybridization and polyploidy are in all likelihood rather common among plants), and they show that there are situations where the individuality thesis is challenged or at least has some unexpected and counterintuitive ramifications. However, the alternative, viewing species as natural kinds, faces many more difficulties, most of all that it does not allow species to be historical entities. Or does it? There have been suggestions that, at first glance at least, might reconcile the two apparently mutually exclusive notions of individuals vs natural kinds. The potential solution is a seemingly contradictory compromise: historical or relational essences[9] (e.g. Griffiths 1999; Okasha 2002; LaPorte 2004; see also Kitcher 1984 who defends his species as sets ontology by granting the possibility that these sets may be historically connected). Without going into details, what it boils down to is this—instead of intrinsic essences (property essentialism), essences are now extrinsic historical relations: species (and other taxa) "are clades that is to say kinds defined by shared descent from a common ancestral group: an individual or group that is a member or part of clade is necessarily a member or part of that clade. Thus biological kinds (species, genera, etc.) do have essential properties, and these are historical rather than intrinsic properties" (Bird and Tobin 2015). Similarly, Ruse (1987, p. 236) says that "[d]escent is starting to look very much like an essential property". This, however, comes at a cost: the boundaries between whole-part relationships of individuals on the one hand and element-kind/class relationships on the other are blurred and entities are multiplied beyond necessity (Ereshefsky 2010b), violating Ockham's famous razor of parsimony. My suspicion is that this is hardly anything more than saying that individuals are natural kinds with historical essences, thus simply expanding the definition of natural kinds to include individuals. If this is true, then nothing of ontological relevance is added by

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[9] Griffiths (1999) calls it "squaring the circle".

this approach; it is a mere terminological trick. There is, however, yet another attempt at rehabilitating the species-as-kinds view that will be briefly discussed in the next section.

3.3 *Tertium non datur*? Species as Cluster Kinds and a Potential Reconciliation of Kinds with Individuals

Apart from historical essences (see above), there is a second kind of recent "new biological essentialism" (Ereshefsky 2010b). Again, this approach is different from the "dead issue" (Sober 1980, p. 353, Stamos 2003, p. 122) of traditional essentialism that is based on necessary and sufficient intrinsic properties of the class or kind that (unlike the accidental or contingent properties of nominal essentialism) are the reason why the kind is what it is.[10] Rather, it is a cluster class or cluster kind approach: "Cluster classes are loosely essentialistic, for although there is a set of defining properties which defines the class, no one property from within that set is necessary or sufficient for membership in the class. Instead, all that is required for sufficiency of membership is possession of a certain minimum number of properties from within that set, a minimum quorum" (Stamos 2003, p. 123). This kind of class is also known as polythetic or polytypic classes. This approach obviously solves the problem, fatal to traditional classes, that no single (intrinsic) property of a species is really essential: a tiger born without stripes is still a tiger, and that pertains to all possible traits one might choose to define the species *Panthera tigris*. What matters is only that the tiger cub shares a minimum number of traits from the pool of tiger traits or, as it is sometimes phrased, that the tiger cub has a higher than chance probability of exhibiting any of these tiger traits while allowing for it not to share all of them. This cluster class approach is usually regarded as being triggered by Ludwig Wittgenstein's concept of *family resemblances* (translation from the German *Familienähnlichkeiten*) in his posthumously published *Philosophical Investigations* (1953). Upon describing what games have in common, Wittgenstein notes

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[10] "Dead issue" because this view is generally held to be obsolete. That probably holds true for philosophically inclined biologists, but there are some philosophers left who insist that species do have intrinsic essences, e.g. Michael Devitt who states: "There has to be something about the very nature of the group—a group that appears to be a species or taxon of some other sort—that, given its environment, determines the truth of the generalization [for example that Indian rhinos have only one horn, while African rhinos have two]. That something is an intrinsic underlying, probably largely genetic, property that is part of the essence of the group. [...] If we put together each intrinsic underlying property that similarly explains a similar generalization about a species, then we have the intrinsic part of its essence" (Devitt 2010, p. 655). Classical intrinsic essentialism is, of course, not compatible with evolutionary change and one species giving rise to another because natural kinds cannot evolve; to reconcile essentialism with evolution, one has to advocate that organisms pass from one kind to another (see Devitt 2008 and, for example, Richards 2010, p. 156f. for a short critical discussion of Devitt's views).

that they are all similar but do not have a single feature that unites them all, concluding (I, 67): “I can think of no better expression to characterize these similarities than ‘family resemblances’; for the various resemblances between members of a family: build, features, colour of eyes, gait, temperament, etc. etc. overlap and criss-cross in the same way.— And I shall say: ‘games’ form a family”. Cluster kinds are a reaction to fuzzy boundaries. Massimo Pigliucci (2003, p. 601), who explicitly embraces Wittgenstein’s family resemblance concept in the context of the species problem,[11] writes: “While scientists tend to be uncomfortable with fuzzy concepts, this is simply a philosophical prejudice: just because we cannot draw a precise line somewhere, it doesn’t mean that there are no distinctions and that everything can be accommodated. Cluster concepts are not at all about abandoning the search for definitions, but they do force our mind to be less rigid about it”.

The most influential cluster class approach in biology is that of Boyd (1991, 1999) who holds that species are homeostatic property cluster (HPC) kinds. Boyd thinks that biological species, just like chemical elements, are “paradigmatic natural kinds, their historicality and lack of sharp boundaries notwithstanding” and “that even those scientists who are convinced that species are individuals must conclude that they are natural kinds as well” (Boyd 1999, p. 141). A succinct summary of HPC theory is given by Ereshefsky (2010b, p. 675): “HPC kinds have two components. First, the members of an HPC kind share a cluster of co-occurring similarities. No similarity is necessary for membership in an HPC kind, but such properties must be stable enough to allow for successful induction. Generally, the aim of HPC theory is to capture groups of entities that share similarities that are projectable and sustain successful induction. Furthermore, the co-occurrence of the similarities found among the members of an HPC kind is caused by that kind’s homeostatic mechanisms. Suppose, for example, that *Canis familiaris* is an HPC kind. The members of *Canis familiaris* share many similar features, such that if you know that Sparky is a dog, you can predict with greater than chance probability that Sparky will have a tail. And, according to HPC theory, the similarities found among members of *Canis familiaris* are caused by that species’ homeostatic mechanisms, such as interbreeding, shared ancestry, and common developmental mechanisms. Proponents of HPC theory see it as a form of essentialism because they believe that HPC kinds perform the inductive and explanatory roles of traditional essentialist kinds (without requiring that essential properties are intrinsic, or necessary and sufficient for kind membership).” According to Wilson (1999a, p. 198), the HPC view “is a ‘cluster’ view twice over: only a cluster of the defining properties of the kind need be present for an individual to fall under the kind, and such defining properties themselves tend to cluster together—that is, tend to be coinstantiated in the world. The first of these features of the HPC view of natural kinds allows for inherent variation among entities that belong to a given natural kind. The second of

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[11] Pigliucci’s application of family resemblance, however, is to the species category, not species taxa (see Sect. 3.6).

these features distinguishes the HPC view as a *realistic* view of kinds from the Wittgensteinian view of concepts more generally to which it is indebted. On the HPC view, our natural kind concepts are regulated by information about how the world is structured, not simply by conventions we have established or language games we play". HPC natural kinds may also be compatible with species evolving: "From the perspective of HPC theory, natural kinds can undergo change, as their defining factors (the property clusters and sets of underlying causal factors) are essentially open-ended. Thus, conceived of as HPC natural kinds species can evolve, and there is nothing in HPC theory [. . .] that is incompatible with evolutionary theory" (Reydon 2009, p. 667).

HPC kinds thus may somewhat soften the otherwise stark contrast between the two opposing ontological categories of individuals and classes or natural kinds that are often held to be mutually exclusive, which is why Boyd thinks that "the debate over whether species are kinds or individuals is less momentous metaphysically and methodologically than one might at first suspect" (Boyd 1999, p. 141). This view, however, is not shared by everyone. Ereshefsky (2001, p. 108) holds that there are serious difficulties with the HPC approach: "We must already know which organisms belong to a species and which homeostatic mechanisms are associated with those organisms. Only after we have that information can the homeostatic approach be used to provide a description of a taxon's characteristics and its homeostatic mechanisms. When applied to species, Boyd's homeostatic approach fails to tell us why certain organisms with certain homeostatic mechanisms are members of a species. In this way, Boyd's homeostatic approach and Wittgenstein's family resemblance account suffer from a similar weakness: they fail to provide an adequate account of what makes the members of a species taxon members of that taxon". Since Boyd allows for historically disconnected lineages to be the same species (cases like the independently arisen hybrids above), Ereshefsky also diagnoses a more fundamental flaw: "The point is that Boyd allows taxa to be noncontinuous entities, and that is at odds with biological taxonomy[[12]]. [. . .] The root of the problem is that HPC theory assumes that all scientific classification should capture similarity clusters. However, that is not the aim of biological taxonomy. Its aim is to capture history" (Ereshefsky 2010b, p. 676).

Rieppel (2007, 2008, 2009), on the other hand, embraces Boyd's HPC theory to reconcile the two opposing views of species as individuals and as natural kinds. And there is an intuitive appeal in that approach. After all, species do show some kind of homeostasis, and not only because of shared ancestry, at least not directly—they undergo similar selection pressures, they have similar developmental constraints and of course, in the case of sexual organisms, they exchange genes which, depending on the extent of gene flow, may homogenize gene pools. So, when looking at a species through time, it might seem that "within" this diachronic lineage, i.e. in each time slice, there is a synchronic homeostatic unit with some

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[12] That may not be entirely true if only taxonomic *practice* is considered (see the case of *Senecio cambrensis* in Sect. 3.2).

degree of cohesion, moving through time, as it were. My guess is that many biologists would subscribe to this intuitive description. I would argue that this description is not wrong, but the issue is a little more complicated than that. The common view of adherents of the individuality thesis is that there is a clear-cut dichotomy between individuals (particulars) and classes (universals); everything is either one or the other; there is no ontological room for anything in between. Rieppel, on the other hand, advocates a somewhat softer distinction between natural kinds and individuals (and many others do, too, including biologists; see Rieppel 2007 for references). He grants, of course, that species are historical entities and that they have a unique origin, "and yet, biologists speak of populations that have a certain allele frequency, or of tetrapods that have four legs, and thus attribute to reproductive communities, or taxa, certain shared properties in a subject-predicate discourse" (Rieppel 2007, p. 375). "But where there are properties, there also are kinds, and where these properties are causally grounded, there are natural kinds. [...] As long as it is admitted that species have causally grounded properties, it also has to be admitted that talk about species as individuals can be translated into talk about species as natural kinds (LaPorte 2004)" (Rieppel 2007, p. 378). Accordingly, species names may function as both proper names (individuality aspect of species) and as general names (natural kind aspect of species). This type of natural kind (Rieppel has HPC kinds in mind) is a weaker notion of natural kinds that allows them to be historically limited and have fuzzy boundaries. This makes it possible to regard species as kinds and individuals (or neither nor, on the view that the two are mutually exclusive) and "avoids the disjunctive opposition of the individuality versus natural kind thesis. Species are spatiotemporally restricted, dynamic and integrated systems, and in this sense are complex wholes, i.e., individuals. But they also possess properties (morphological, physiological, genetic, etc.), causally efficacious behaviours (social, migratory, predatory, etc.) and causal powers (reproductive, competitive, etc.) that are variable and temporally bounded, but still identifiable and re-identifiable not only by biologists, but by the species themselves. [Therefore,] species are also of some kind, each being one of its kind. [...] What counts is that the kind-constitutive properties make the token organisms that 'belong to' a species sufficiently similar to each other and sufficiently dissimilar to those of other species to allow generalizations about the species and its parts, their properties, their causally efficacious behaviors, and their causal powers with at least some significant degree of reliability [...] i.e., better than chance predictability" (Rieppel 2007, p. 382f). Species are thus the single members of their own specific natural kind, and properties of species are identified as parts of the whole which is in line with natural kinds (in the weaker notion advocated by Rieppel) being historically delimited. In a nutshell, Rieppel characterizes species as "complex wholes (particulars, individuals) that instantiate a specific natural kind" (Rieppel 2007, p. 373) or as "open or closed, causally integrated processual systems that also instantiate an historically conditioned homeostatic property cluster natural kind" (Rieppel 2009, p. 33). Although quite complicated, this may be a promising approach to accounting for and softening the tension between different aspects of what we perceive as "species-ness". Of course, this comes at a price[13]—the strictly dichotomous distinction between the two mutually exclusive basic ontological categories of individuals and classes is not so clear-cut anymore but has become a lot fuzzier. Since fuzziness, however, is something like a leitmotif when dealing with the species problem, it may not be so surprising after all if it also lurks in its ontological aspects. Acknowledging this, Michael Ruse concludes: "Evolution over time and space is not something our ancestors encountered. We tend to make mathematical objects like triangles—things with clean and clear definitions—as our paradigms of the objects of classification. Humans, tigers, artichokes are treated the same way. So, if Darwin is right and you have to think of groups as fluid, non-permanent, there is bound to be a breakdown. The species problem is a fascinating problem, but in the end it may be a waste of time to try to force species to be more than they are. They are objective, but only so far. Leave it at that" (Ruse 2008, p. 137). I do not think, though, that "leaving it at that" is a satisfactory option. What may be more promising is to think along the lines of the first part of Ruse's quote, and this is exactly what in particular Jody Hey has done when he started looking for potential cognitive causes of the species problem, to which we now turn.

3.4 The Cognitive Causes of the Species Problem: An Epistemological Hypothesis

Studies of biological folk taxonomy, the traditional vernacular naming and ordering system of living beings by people, have yielded fascinating results: people from very different regions on earth intuitively classify living beings in a very similar manner, and there is a varying but undeniable overlap of these folk classifications with scientific biological classification (e.g. Berlin et al. 1966; Atran 1990, 1999). Never mind that folkbiological "species" are often more similar to the level of genera in scientific classifications; this seems good evidence that the depicted entities are real, proving species taxon nominalism wrong. Indeed, the independent but congruent folk classifications have been interpreted in exactly this way, for example, by Ernst Mayr: "I have always thought that there is no more devastating refutation of the nominalist claims than the fact that primitive natives in New

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[13] And not unexpectedly, Rieppel's approach at a reconciliation has been criticized, e.g. by Reydon (2009). Among other things, Reydon (2009, p. 666) criticizes that the reconciliation of kinds and individuals is not a real one but only works on the epistemological but not on the metaphysical (ontological) level: "What philosophers usually mean when asserting this [that kinds and individuals are not mutually exclusive] is that *from an epistemological point of view* the two views are compatible, in the sense that reference to species names in biological reasoning can function to denote kinds or individuals. Most authors who endorse the compatibility of the two views also do not hold that the two views *as metaphysical statements* are compatible—that species *are* both individuals and natural kinds".

Guinea, with a Stone Age culture, recognize as species exactly the same entities of nature as western taxonomists" (Mayr 1988, p. 317, quoted from Stamos 2003, p. 95). However, this is a naïve interpretation in the eyes of many: "the fact that independently observing humans see much the same species in nature does not show that species are real rather than nominal categories. The most it shows is that all human brains are wired up with a similar perceptual cluster statistic" (Ridley 1993, p. 404). Ridley is right: congruence in perceiving species does not make species any more real than optical illusions that all humans perceive but that we know differ from objective reality. Similarly, the fact that we perceive time and space in accordance with Newtonian physics doesn't mean this is correct—in fact, since Einstein we know that this is only an approximation. Assuming the reality of species taxa is well-founded, but folk taxonomy is not a good argument for it. But perhaps there is something else to be learned from the consistency with which humans classify living beings, about our cognitive constraints and how these might shed light on the origin of our problems with species. Jody Hey (2001a, b) basically argues that humans are programmed to approach the world through pigeon-holing. Inspired by Willard V. O. Quine's *Word and Object* (1960), his starting point is the friction between our discrete language and a largely continuous nature. This point will come up again in Chap. 6 about species delimitation as the discrepancy between discrete taxonomy and the continuousness of the evolutionary process. Nature is fuzzy, and the Tree of Life has a fractal structure (lineages within lineages within lineages and so forth like a Matryoshka doll): "If biodiversity is fractal, then we would expect that one could always find a finer pattern within a pattern, a smaller group within a group, except in the not very useful limit wherein basal taxa include just individual organisms" (Hey 2001a, p. 86). As a consequence, vagueness will always be inherent in species concepts (as it is inherent in other concepts like clouds, diseases, life or gene), but this is nothing to worry about as it reflects reality: "There is no harm, nor paradox, in embracing a term that conveys an idea of potentially uncertain boundaries when in fact that is precisely the nature of the things to which we refer" (p. 171). Hey holds that our mind is programmed to think in terms of categories that arise as generalizations from recurrent patterns that we perceive, i.e. we cannot but view species as categories because this is how our cognitive capacities evolved. Scientific insights about evolution and the historical nature of species have made us realize that species are natural entities, not abstract categories, but our brains are still pigeon-holing, resulting in a cognitive conflict: "In brief, modern biologists suffer two imperatives. The first is the ancient one of all people and that is to devise categories and invent just as many kinds of organisms as we want or need to give voice to our thoughts about that diversity. The second is to understand the causes of that diversity. Indeed, our pursuit of that second imperative has been so successful that is has given us a species problem" (Hey 2001a, p. 108). In other words, we now know that species as we perceive them have two causes: "(1) the evolutionary processes that have caused biological diversity; and (2) the human mental apparatus that recognizes and gives names to patterns of recurrence" (Hey 2001b, p. 328). The cognitive dimension of the species problem is therefore similar to the cognitive dissonance between classical mechanics (the perceived Newtonian structure of time and space) and relativistic mechanics according to Einstein, when velocities are not insignificant compared to the speed of light. Our mental apparatus's evolution did not include dealing with objects that quick, and something analogous holds for our way of classifying nature: "Our perceptions are not a perfect mirror of nature. [. . .] There is no reason why our senses should be as capable of the same subtleties as can arise in nature" (Hey 2001a, p. 109). We should not expect, therefore, that our minds perceive entities in nature in accordance with evolutionary theory: "Our categories of organisms are good tools in many ways, but they come up short in the face of modern demands that they match our understanding of evolution. Even as our categories fail us we still cling to them, which is another way of describing the cause of the species problem" (p. 110).[14] Hey diagnoses in us "a predisposition to misunderstand species" (p. 66) and calls biologists "knowingly biased scientists" because "the human mind is predisposed to refer to kinds of organisms in a manner that draws on mental structures that are inaccurate representations of the reality that causes those perceptions" (p. 65)—and we know this! Categorical or essentialist thinking is a fundamental aspect of our minds: the capacity for language is based on the capacity to learn, and learning proceeds as a recurrence cycle, and recurrence results in categorical thinking (p. 121). Our goal, then, must be to disentangle the real evolutionary entities (the E species) from the categories as which species are represented in our minds. Most species are diagnosed and named as T species, and they are probably more often than not based on the categorical perception that we have of species, which is why T species are at best hypotheses of E species. Hey views the real evolutionary entities, the E species, as an ultimate cause of the species categories in our mind, but often the two do not match exactly, and that is due to our cognitive limitations: "Evolutionary groups are just one major cause of our species taxa, and we are the other" (Hey 2001a, p. 157). Although, strangely, Hey never mentions Kant as far as I can see, this is of course very Kantian in that the objectively real thing (the E species in this case, the *Ding an sich* or "thing-in-itself" in Kant's epistemology) is perceivable only through the mediation of our cognitive powers, and what we eventually perceive is a hybrid of both. So, where does this leave us? Hey has not solved the species problem, and he never claimed that that was his aim, but he has perhaps shed some light on why species are so slippery and elusive by showing us, if indeed he is right, that part of the problem lies in the way our cognitive apparatus works. The aim is still to find real entities, but "[t]here is simply no other avenue open to us, for considering organisms as parts of entities, that does not first pass through having treated them as a category" (p. 181), and

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[14] This is one of the central tenets of evolutionary epistemology—our cognitive powers evolved in adaptation to our surroundings, but this does not imply a perfect match, of course. Surviving and reproducing was enough; the pursuit of complex scientific issues was not directly selected for. Still, our cognitive and sensory apparatus must mirror the very structures it perceives in some, albeit imperfect, way—and it does, as beautifully encapsulated in the famous lines by Goethe "Wär nicht das Auge sonnenhaft/Die Sonne könnt es nie erblicken" ("Were the eye not like the sun/The Sun it never could behold").

from this Hey derives a “litany” for biologists: “Do not mistake categories for entities; do not mistake taxa for real species; taxa are mental categories that correspond to patterns in the world, and they are not evolutionary groups” (p. 182). Hey is very sceptical whether it is possible at all to arrive at a taxonomy where taxa and natural entities are one and the same, but one does not have to follow him in all that he claims to subscribe to this warning—being aware of the pitfalls of T and E species will certainly make us better biologists.

3.5 Species as Relations

David Stamos (2003) has recently introduced a new suggestion about the ontology of species that resulted in his biosimilarity species concept (see Chap. 4). Following particularly Bertrand Russell in taking relations (and not just objects) seriously and for real, he challenges the simple dichotomy of species as classes or natural kinds vs species as individuals. Stating that universals, contrary to common notions, come in two kinds, properties and relations (the latter usually being neglected), he holds that species are “a complex of similarity relations (with organisms ultimately as the relata) objectively bounded or limited by various causal relations (such as interbreeding relations, ecological relations, ontogenetic relations, caste relations, etc.). I call this the *biosimilarity species concept*” (Stamos 2003, p. 25). To Stamos species as relations is an ontological “hybrid category” (p. 289) that is a fusion of both the abstract and the concrete because relations, at least according to Stamos, include their relata (the particulars among which the relation exists). This way, similarity relations are not abstract classes, and species can evolve and be real entities existing independently of the human mind. However, precisely since he is including the organisms together with their relations into his definition of species, this approach is perhaps not so novel after all but collapses into a rather traditional position like “species are concrete objects whose component organisms bear certain similarity relations to one another” or something along these lines (LaPorte 2006, p. 384). Some ramifications of this view are the ontological superiority of horizontal over vertical species, that one and the same species can originate several times (e.g. through repeated polyploidization or hybridization of the same parental species) and that extinction, therefore, is not necessarily forever. To many if not most biologists, these consequences are hard to swallow, and the fact that similarities are the defining part of species—not a consequence of organisms being part of the same species and thus a means to identify them—is in stark contrast to most notions of species in evolutionary biology. Accordingly, Baum (2004) considers Stamos’ book “too detached from modern evolutionary thought to be of much use to biologists” (p. 64; while he also thinks that philosophers of biology should read it). His view on the biosimilarity species concept is that it is “incoherent and completely unworkable” (p. 64) and “little more than a post hoc philosophical justification for assorted traditional practices” (p. 65). This may be a little harsh, but as far as I can see, neither the ontological notion of species as relations nor the biosimilarity species concept that follows from it have met with much response, let alone approval, since their publication—either from biologists or philosophers. As much as biology is concerned, to me this seems to be the case because Stamos's similarities create more problems than they solve and, most importantly, because they are not in accordance with how modern evolutionary biology has come to view species, and that is first and foremost as historical entities in the form of independent population-level lineages.

3.6 Species Pluralism and Species Category Nominalism: Denying the Existence of a Single or of Any Species Level

As already briefly outlined in Sect. 1.5, species pluralism is the position that there are different kinds of species, i.e. that there is no single correct definition of the species category but rather several depending on the taxon or topic under study. According to this view, then, there would be, for example, ecological species, biological species, evolutionary species, etc., each in their own right and each equally real. On this view, the discussion about which species concept is the one that objectively "carves up nature at its true joints" is moot or misguided. A view deviating even more strongly from the standard notion that there is a single best species concept is a variety of species nominalism. Species *taxon* nominalism, the view that species taxa like *Homo sapiens* are but constructs of the human mind that do not exist outside our brains, is defended by fewer and fewer biologists and philosophers. But acknowledging the reality of the entities/lineages that we call species does not necessarily entail the reality of the species rank. In other words, while species taxa may be real entities, these entities may still be very different from one another and not share a common denominator by means of which the species category could be unequivocally defined. Species taxa on this view would be as real, but also as different, as apples and oranges. This would make species taxa incommensurable, and the fact that they are all called species would be misleading because the same name would be given to very different things.[15] Let us turn to

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[15] Stamos holds that it is logically doubtful to consider species taxa as real but not the species category (as we have seen he also argues that Darwin was a realist with respect to both). His argument is this: "no species category, no *species* taxa. In other words, if one believes that species taxa are real but not the species category, then the very phrase 'species taxa' becomes a contradiction in terms" (Stamos 2003, p. 94). With all due respect, I can hardly see anything but a logical sleight of hand or even sophistry in this. First of all, the argument ignores the distinction between T and E species: everything with a binomial is by definition a taxonomic species. Whether this is appropriate or not is irrelevant in this context; at least in this regard, entities can always be called species. Species then does not mean anything more or less than being taxonomically acknowledged and having a binomial. Apart from this, the use of the name species for species taxa when there is no species category is a pure matter of tradition and could be abolished in favour

species pluralism first and have a brief look at it. Reydon (2004; see also Mishler and Brandon 1987) emphasizes that there are actually two kinds of species pluralism, “two overarching (but not sharply delimited) types”. One, the more radical version, “holds that the species concept can be broken down into a number of—to some extent—independent subconcepts that can be applied to *the same* organisms depending on the question under consideration. Ereshefsky, for example, holds that ‘An organism may belong to two different types of species at the same time. For example, a single organism may belong to both an interbreeding species and a phylogenetic species even though those species are not fully co-extensive’ (Ereshefsky 1998, p. 106). This type of pluralism has also been prominently advocated by philosophers such as Dupré (1993) (although in later work Dupré took a less radical position (Dupré 1999, p. 18) and Kitcher (1984). The other, less radical, type of species pluralism is purely definitional in nature; this form of pluralism is advocated by, among others, Mishler and Brandon: ‘a single, optimal general-purpose classification exists for each particular situation, but (...) the criteria applied in each situation may well be different’ (Mishler and Brandon 1987, p. 403; see also Mishler and Donoghue 1982). Here it is not the case that there are several distinct species concepts that can be applied to the same organisms depending on the research question at stake, but rather there are several different definitions of the concept of species that each apply to particular organism groups for all research questions that can be considered with respect to these groups. This less radical type of pluralism is only pluralist insofar as it allows the existence of different kinds of species; in holding that these different kinds of species exist in different regions of the organismal world and that every organism belongs to precisely one species, it is a monist rather than a pluralist position” (Reydon 2004, p. 303). Doubts that there is a single best species concept are widespread. Edward O. Wilson, while championing the Biological Species Concept as the best and most powerful one, thinks it is “unlikely that a completely universal species definition will ever be fashioned. Instead, two to several concepts will continue to be recognized, like the waves and particles of physics, as optimal in different circumstances” (Wilson 1992, p. 46). On the other hand, Stamos (2003, p. 355) holds that species pluralism presupposes species (taxon) nominalism, but that is contentious, and it does certainly not apply to the “lighter” version of pluralism as outlined by Mishler and Brandon above. It is also noteworthy in this context that LaPorte (2006) thinks that Stamos’ own approach is rather pluralistic than monistic. The position of a less radical pluralism is also adopted by many when it comes to sexual vs asexual species: many researchers think that these two are not the same kind of entities, that asexual taxa do not have species in the same sense that sexual

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of something else (basal lineage, etc.). In fact, the debate about whether there are no species but, for example, only monophyletic groups at different levels (Mishler 1999) suggests that we could get rid of the term species altogether. This, however, does not preclude the reality of lineages (taxa), only of rank (species category) (see also Ereshefsky 2010a).

organisms do but are (in this sense of the word) “species-less” and/or should be given a different name like “agamospecies” (see Sect. 5.1).

One of the most ardent adherents of species pluralism in its stronger version is Marc Ereshefsky (1998, 2001, 2010a). Ereshefsky calls the kind of pluralism he advocates “tempered pluralism”, which is a “substantive middle ground between taxonomic anarchism and taxonomic monism. [... It] allows that more than one taxonomic approach may be worthy of pursuit” (Ereshefsky 2001, p. 163). His pluralism, as he emphasizes, is not just epistemological, but ontological or metaphysical. This means that it is not about a single set of entities (the true species) that can be classified in a variety of ways, but that there really are different kinds of such entities: “All of the organisms on this planet belong to a single genealogical tree. The forces of evolution segment that tree into a number of different types of lineages, often causing the same organisms to belong to more than one type of lineage. The evolutionary forces at work here include interbreeding, selection, genetic homeostasis, common descent, and developmental canalization [...] The resultant lineages include lineages that form interbreeding units, lineages that form ecological units, and lineages that form monophyletic taxa” (Ereshefsky 2001, p. 139). The result is “a multiplicity of classifications that cross-classify the organic world” (p. 135), but this is due to evolution itself because “the forces of evolution segment the tree of life into varying and opposing classifications. Species pluralism is the result of a fecundity of biological forces rather than a paucity of scientific information” (p. 140). On this view, species pluralism is actually a virtue, not a nuisance, and the only appropriate solution to the complexity of the organic world: “Each species approach [interbreeding, ecological and monophyletic lineages] highlights an important component of evolution: sex, selection, or genealogy. A biological taxonomy fashioned on only one species approach neglects significant aspects of evolution. In doing so, it provides an impoverished picture of life on this planet” (p. 143). Ereshefsky embraces the species-as-individuals ontology in that he concedes that species are spatiotemporally continuous lineages, but he denies that there is only one kind of such lineage; instead, he asserts that there are “different types of lineages called ‘species’” (Ereshefsky 2010a). In so doing, he also objects to the solution to the species problem offered by Mayden (1997, 1999) and de Queiroz (1998, 1999, 2007) which are based on a consensus that species are first and foremost lineages (see Sect. 5.2) because this, on Ereshefsky’s pluralistic view of lineages, masks that “what constitutes a lineage has multiple answers, and those answers vary according to which species concepts one adopts” (Ereshefsky 2010a).

Reydon (2005, p. 155) has criticized species pluralism (and other aspects of the species debate) on the grounds that they “rest on a mistaken understanding of the nature of the species question as involving just one scientific concept. [...] the umbrella term ‘species’ covers more than one distinct scientific concept. That is, the term ‘species’ is a homonymic term that stands proxy for a number of independent scientific concepts that, throughout the developmental history of biological science, have come to be called by the same name, but are applicable in different contexts of biological investigation where they perform different roles and refer to different ontologies”. Consequently, species pluralism “not only encompasses but *presupposes* that a basic level of similarity is present between all the concepts denoted by the term 'species' with respect to their ontology, their roles within scientific theory, or both. (Pluralism, after all, is a meaningful position only with respect to things that in some respect are all of the same kind)" (p. 152). Reydon distinguishes four such different and independent ontological concepts, two entity and two class concepts, that are subsumed under the term species (p. 142):

evolveron—"a category of dynamical process entities composed of synchronously living organisms; evolverons are populations or systems of populations that participate as cohesive wholes in evolutionary processes";
phylon—"a category of historical pattern entities, that is, passive products of evolution; phylons are the basic segments of the phylogenetic tree of life";
organism-kind—"a category of classes of organisms; organism-kinds are classes of organisms that exhibit similar structural and/or behavioral properties";
evolveron-kind—"a category of classes of evolverons that occupy similar positions in evolutionary dynamics".

He then assigns different species concepts to these four categories (his Figure 1, p. 142). For example, the Morphological and the Phenetic Species Concepts belong to the organism-kind category; the Ecological Species Concept and the concept of Evolutionarily Significant Units to the evolveron-kind category; the Biological, Recognition, Cohesion and Genetic Species Concepts to the evolveron category; and the Evolutionary, Hennigian, Cladistic and Phylogenetic Species Concepts to the phylon category. I will not discuss this in any detail and completely neglect the two class concepts, but I will briefly comment on the first two concepts, the evolveron and the phylon. It is quite obvious that these two reflect the synchronic or horizontal and the diachronic or vertical dimensions of species. Calling these two ontologically different seems to be fundamentally flawed (see the rejection in Sect. 1.4), and I do not think that many biologists would subscribe to the homonymity claim by Reydon in this regard. The difference between the two class concepts and the two entity concepts is perhaps the same as the one diagnosed by Hey (see Sect. 3.4)—cognitive categories as a result of how our brains work vs natural entities that exist independently of the human observer.

While species pluralism, with or without cross-classification of the same organisms, acknowledges two or more different kinds of species, there is another approach that denies the existence of something like a general species level or rank altogether: species category nominalism (see, e.g. Nelson 1989; Vrana and Wheeler 1992; Ereshefsky 1999, 2010a; Hendry et al. 2000; Pleijel and Rouse 2000;[16] Mishler 1999; Zinner and Roos 2014 are also sympathetic to this view). This view is most often found among cladists who discuss the units of phylogenetic analysis. The basic argument is as follows: in nature, there are single organisms, perhaps populations of single organisms, and at a higher level than this, there are

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[16] Pleijel and Rouse (2000) suggest to get rid of the term species and instead use least-inclusive taxonomic unit (LITU) for the lowest (based on present phylogenetic knowledge) monophyletic group (see also Chap. 4). Wilkins (2009a, p. 221ff.) calls this species "replacementism" and does not see any new insight, just a change in terms.

only taxa that are monophyletic groups of organisms. None of the various levels of inclusiveness are in any way superior to others and thus do not deserve to be singled out as the species level. The species rank is, on this view, not different from all the other Linnean ranks like families, orders or phyla that have long been known to be artificial: the species problem is insoluble because it stems from "a false assumption: that there is an empirical difference between species and other taxa" (Nelson 1989, p. 74). Mishler (1999) concurs with this: "we have no and are unlikely to have any criterion for distinguishing species from other ranks in the Linnean hierarchy, which is not to say that particular species taxa are unreal. They are real, but only in the sense that taxa at all levels are real. Species are not special" (p. 309); "the species rank must go the way of all others" (p. 312), and "species are not comparable in any important sense and cannot be made so" (p. 313). Mishler denies that species can be distinguished from other taxa as the hierarchical point in the Tree of Life where "within-kind" relationships dissolve into "between-kind" relationships (the tokogeny/phylogeny divide according to Hennig), although one might argue that the fuzziness of this boundary does not mean that it does not exist (see Sect. 6.2 for a discussion). He suggests that species in a completely rank-free classification be treated like personal names in Arabic culture: "Each clade, including the least inclusive one named, has its own uninomial name; however, the genealogical relationships of a clade are preserved in a polynomial giving the lineage of that clade in higher and higher groups. Therefore, the familiar binomial, which does after all present some grouping information to the user, could be retained, but should be inverted. Our own short clade name thus should be *Sapiens Homo*. The full name for our terminal clade should be regarded as the polynominal that gives the names of the more and more inclusive clades all the way back. To use the human example, this full name would be something like *Sapiens Homo Hom[in]idae Primate[s] Mammalia Vertebrata Metazoa Eucaryota Life* [...]. Again, as in a traditional Arabic name, this formal and complete name would be used only rarely and for the most formal purpose" (Mishler 1999, p. 312). This suggestion sounds very unfamiliar, but if there really is no distinct species level, it is a very reasonable solution. If species are indeed no different from the higher taxa in that their rank is artificial, then they are just as much subject to what has been called tree thinking (e.g. O'Hara 1997; Baum et al. 2005; Omland et al. 2008) as are higher taxa. That would also mean that all comparisons of species numbers would be flawed, as would be conclusions drawn from them (see Chap. 7)—just as quantitative analyses based on higher ranks (numbers of genera, families or orders, etc.) suffer from the apples and oranges problem (e.g. Bertrand et al. 2006; Zachos 2011). This would not make such analyses impossible, rather it would make them more precise: "comparisons among clades would still be quite feasible, but it would be up to the investigator to establish that the clades being compared were the same with respect to the necessary properties (i.e., equivalent age or disparity, and so on). [...] rank-free classification would lead to much more accurate research in ecology and evolution because investigators would be encouraged to use cladograms directly in their comparative studies instead of relying on equivalence in taxonomic rank as a (very) crude proxy for comparability of lineages" (Mishler 1999, p. 313). While this is not new with respect to higher ranks, it would now also apply to species. This, however, hinges on whether there really is no objective property that distinguishes the species rank from all the others. Whether the species rank can be used in quantitative analyses in a meaningful way is a question whose relevancy can hardly be overestimated. If species pluralism, particularly in its more radical form that allows for cross-classification of the same organisms, were an adequate description of the living world, or if the species category as a whole did not exist, this would have very serious consequences for any scientific endeavour that uses species, particularly species numbers, as data: "when it is asked how many species there are in the world, the question is not what somebody might want to call species, but how many units of a given kind do in fact exist. A pluralistic species concept renders such an effort altogether worthless. Imagine what would happen if the United States Bureau of the Census attempted to do its job with a 'pluralistic' conception of 'inhabitant' and instead of everybody collecting the data counting heads, one census taker were to count heads, another legs, another digits, perhaps others hairs" (Ghiselin 1997, p. 120). This would impact not only evolutionary biology and ecology but also conservation and management. That species pluralism and species category nominalism would render many analyses biased or even pointless, however, is of course not an argument against their being correct. Still, it is a very alarming prospect that will be taken up in Chap. 7.

A potential way out of the (theoretical) aspects of this predicament has been shown by Massimo Pigliucci (2003), drawing on earlier ideas of Hull and the numerical taxonomists. He suggested to view the species category as a family resemblance concept and compares the species category to the category of games in Wittgenstein' s philosophy (see Sect. 3.3). What is important is that Pigliucci's approach refers to the species *category*, not the species taxon. The latter has also been interpreted as a cluster class, e.g. in the homeostatic property cluster (HPC) theoretical approach by Boyd (Sect. 3.3). The species category has always been considered to be a class (the class of all species taxa), but usually in a more traditional way with fixed defining properties that are the content of the various species concepts. Pigliucci now moves away from a strict and narrow definition of the species category and allows for a number of property conditions not all of which have to be met. Pigliucci identifies "broadly speaking only three factors entering into the equation: phylogenetic relationships, genetic continuity (sometimes specifically concerned with reproductive traits, sometimes more broadly defined) or similarity, and ecological similarities, broadly construed" (Pigliucci 2003, p. 598), and accordingly he regards the species category as a "family resemblance concept whose underpinning is to be found in a series of characteristics such as phylogenetic relationships, genetic similarity, reproductive compatibility and ecological characteristics. These traits take on more or less relevance depending on the specific group one is interested [in] as a function of the particular biology of that group" (p. 601). Among the "conventional" species concepts, Templeton's cohesion concept (see Chap. 4) comes closest to this approach in Pigliucci's view, "especially if a phylogenetic component is appropriately factored into it" (p. 601). Pigliucci also sees the species category family resemblance idea as compatible with Hey's theory that there is a fundamental dichotomy between categories produced by our brains and real natural entities, and it "at once erases the need for endless squabbles among biologists on what *the* best species concept is. The concept is fluid (but not arbitrary!) and gains enough flexibility to be applicable to the variety of real biological cases" (p. 601). On the other hand, Pigliucci emphasizes that the family resemblance approach is fundamentally different from species pluralism: while the latter entails the existence of "equally legitimate, *conceptually independent*, species concepts that can be used depending on the interest of the investigator", according to the former "species represent one large cluster of natural entities, quite independently of the interests of human observers. This cluster, however, is a loose one, with its members connected by a dense series of threads, not all of which go through every single instantiation of the concept" (p. 601). From a philosophical point of view, this sounds very convincing. However, whether this is more than a theoretically sound appeasement for the biological side of the coin is probably an open question. Species taxa according to different subsets of the cluster class that the species category is on this view may still be considerably different, and lumping them together in analyses based on species counts would still create an apples and oranges problem.

3.7 Species Ontology and Type Specimens in Taxonomy

The fact that species are historical entities and therefore individuals (whatever else they might be) has important implications for the type concept in taxonomy. The term type has been used in various different meanings, and the fact that typology has come to be used as a synonym for essentialism has not helped clarification. Farber (1976), who gives a nice overview of different usages and interpretations of type concepts in the nineteenth century, distinguishes three different kinds: classification, collection and morphological type concepts. The first refers to the use of a member of one taxon as a characterization of the next higher taxon (e.g. a type species for a genus), and the last is a somewhat vague notion of a morphological plan at a certain taxonomic level (and sometimes interpreted as a variation on an archetype). The collection type concept is the "conventional name carrier" and refers "to a set of specimens that ha[s] been used by authors in establishing new species" (Farber 1976, p. 116). While the classification type concept with its type species as name-bearing types of genera and type genera as name-bearing types of families is still used, officially or unofficially, in present-day nomenclature, the most important usage of types lies in their being the very specimen(s) based on which species (or subspecies) have been and are being described (holotypes, paratypes, etc.). Under an essentialist paradigm, these specimens could function as an instantiation of all the properties defining a species. However, as we have seen, species have neither instantiations nor defining properties. What, then, is a type? It really is just a name carrier, the very specimen that was used in the ostensive "definition", the act of christening, of a species: "The properties of organisms can be used to describe, or to diagnose, their species, but the name of the species itself has to be defined ostensively, and in formal taxonomy this is accomplished by type designation" (Ghiselin 1997, p. 304). Therefore, types need not be typical in the usual sense of the word—quite to the contrary, type specimens can be morphological outliers or aberrations. Types do not even have to be parts of an organism of the species it refers to: trace fossils (such as footprints or borings) or bird nests can also function as types—"and that ought to clinch matters" (Ghiselin 1997, p. 67—in favour of types being carriers of proper names). Thus, types are not typical examples of a species, and they do not by definition display all the species' characters; they are merely the "material result of an act of baptism", as it were. They represent the name (not the properties) of a T species. The decision whether a given organism belongs to the same E species as the type is actually a difficult one: one would have to show that the organism under study belongs to the same historical biological entity as the type specimen—not an easy task! So what one usually does is to assume that a certain (but fuzzy and ultimately conventional) degree of similarity is the yardstick by which the decision is made. This holds for both morphological comparisons and more recent molecular techniques such as DNA barcoding (Hebert et al. 2003) where a particular gene (for the animal kingdom mostly the cytochrome c oxidase subunit I, or COI, gene) is sequenced that is known to be much less variable within what are considered species than among them; i.e. intraspecific genetic distances do not overlap with interspecific genetic distances ("barcoding gap").

I have heard type specimens being compared to the international prototype kilogram in Paris (and I admit to having made that comparison myself), but except for a very superficial similarity (both are unique reference specimens that are used ostensively), this comparison is flawed: the prototype kilogram (the very platinum-iridium cylinder kept in Paris) is not part and name carrier of a historical entity with the proper name kilogram, whereas taxonomic-type specimens are exactly that! That something as important as the basic unit of mass is defined ostensively by means of a reference specimen is highly unsatisfactory, of course, and the equivalent of the prototype kilogram for length, the platinum bar that used to be the international prototype meter or *mètre des archives*, has been replaced by a definition of one meter based on the speed of light in vacuum. Ostensive definitions are definitions by pointing out examples. In the case of general categories (classes), ostensive definitions are unsatisfactory and should be replaced by real intensional definitions. In the case of proper names, however, an ostensive definition is all one can achieve.

3.8 Concluding Remarks

Although this chapter on the ontology of species has eventually become much longer than I initially had intended it to be, it is still only a very brief summary of the debate. Countless more publications on the topic are available, and interested readers might turn to the ones I have cited and look for references within them. The journal *Biology and Philosophy* published a themed issue on species ontology (vol. 2(2) in 1987) starting with two papers by Michael Ghiselin and Ernst Mayr on which a number of other authors (incl. David Hull, Mary Williams, Philip Kitcher and George Ledyard Stebbins) then comment, followed in turn by responses from Ghiselin and Mayr. Some of the papers of this special issue have been cited in this book, but not all, and readers may be interested to read those as well.

The issue is complex, and many of its aspects are not of immediate relevance for biologists at large. Some, however, are of utmost importance. Species are, whatever else they might be, necessarily historical entities and, at least in this sense, individuals. This means, and that is probably the most important conclusion and take-home message for biologists, that species (and higher monophyletic taxa) cannot be *defined* by properties—they can only be identified by them. As Hull (1976, p. 190) put it in one of his early individuality papers: "at the very least, species are not classes. Spatiotemporal continuity is necessary for species to function as units in the evolutionary process. Whether or not spatiotemporal continuity is also necessary for something to be an individual, it is sufficient for not being a class". In line with this, I do not think there are many biologists left who consciously regard species as classical natural kinds with essential intrinsic properties. My personal view on this issue is that Ghiselin, all criticisms and philosophical "sleights of hand" like historical essences notwithstanding, is right—species are spatiotemporally restricted historical entities without defining properties; they can only be defined ostensively and therefore have proper names. Ghiselin calls these entities individuals, and I think legitimately so. If the issue of cohesion or a particular kind of cohesion is perceived as integral to the term individual, one might choose another one, but regardless of terminological questions, I think that species cannot be classes, not even natural kinds in the usual sense of the word. Such an ontology of species would not and could not be in accordance with evolutionary theory and the historical nature of the Tree of Life. A reconciliation between natural kinds and individuals as outlined above by Rieppel is an interesting suggestion and may well hold but (and this is important) species on this view are still historical entities, not conventional classes. That is the minimum conclusion that biologists should draw; the rest is rather complex philosophy and perhaps not directly relevant to biologists for their daily work. The compromise outlined by Rieppel does, however, rehabilitate properties and similarity to some degree, and it offers reason to not feel guilty about viewing species also from that perspective, as long as one keeps in mind their historicity as well.

Finally, it may also be worth noting that the view that species are individuals (or at least cannot be classes or natural kinds that have essential properties) has important ethical ramifications. If species have no essential properties, then there is strictly speaking no such thing as human nature (Ghiselin 1987a, 1997, p. 1), which means that no human being or group of human beings can be discriminated against on the grounds that they "participate less" in human nature and therefore are of an inferior humanity: "There may be characteristics which all and only extant human beings possess, but this state of affairs is contingent, depending on the current evolutionary state of *Homo sapiens*. [. . .] Some people may be incapable of speaking or understanding a genuine language; perhaps bees can. It makes no difference. Bees and people remain biologically distinct species. [. . .] Possibly women and blacks are human beings but do not 'participate fully' in human nature. Homosexuals, retardates and fetuses are somehow less than human. And if bees use language, then it seems we run the danger of considering them human. The biological interpretation has much to say in its favor, even from the humanistic point of view" (Hull 1978, p. 358).

Chapter 4
An Annotated List of Species Concepts

There are about 30 species concepts in the literature. The exact number depends on what one considers a full or acknowledged concept (sometimes a comment or definition in the literature may not be called a concept and/or may not have made it into the canon of "official" species concepts), and it also depends on where one draws the line between similar or nearly identical concepts. The list below of 32 species concepts is therefore neither exhaustive nor the only way of listing species concepts. I mainly follow Mayden (1997, 1999), the list in Wilkins (2009b) which is based on Wilkins (2006a) and Wilkins's website http://scienceblogs.com/evolvingthoughts/2006/10/01/a-list-of-26-species-concepts/ (Wilkins 2006b) but have included the General Lineage Species Concept and the Unified Species Concept by de Queiroz (1998, 1999, 2005b, 2007), added Stamos' (2003) Biosimilarity Species Concept, Baum and Shaw's (1995) Genealogical Species Concept and finally the Differential Species Concept and the Pragmatic Species Concept which were published more recently (Hausdorf 2011; Seifert 2014). I also sometimes use slightly different names than those given in other lists.

It should be kept in mind that species concepts are definitions of a class, i.e. they refer to the class of all entities that we call species. They define the species *category*, while the entities that fall within this category are the species *taxa* (which are logical individuals; see Chap. 3). I will not discuss all species concepts in detail but will highlight and discuss a number of particularly widespread and important concepts in sections of their own in Chap. 5.

It will be obvious that some species concepts are very similar or even hybrid concepts with mixed criteria. It is tempting to give a classification of species concepts and combine related concepts into groups, e.g. all species concepts based on reproductive isolation (Biological Species Concept, Recognition Species Concept, Hennigian Species Concept and others), on phylogenetic/cladistic theory (Cladistic Species Concept, various so-called Phylogenetic Species Concepts), etc. A functional hierarchical classification of species concepts is presented in a figure by Mayden (1997, 1999) when he explains primary (ontological) and secondary (operational) species concepts (see Sect. 5.2) and shows which of the operational

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species concepts function as species identification criteria in different biological situations (gene flow present or not, sexual or asexual reproduction, etc.). Another way of grouping species concepts is based on whether they are based on evolutionary processes or on patterns (i.e. the result of such processes). The former would include concepts like the Biological, Recognition and Ecological Species Concepts, while the latter comprise, among others, the Morphological and the Phenetic Species Concepts as well as the diagnosability version of the Phylogenetic Species Concept. Yet another approach at classifying species concepts is to distinguish those that define species in a single time horizon ("horizontal" concepts like the Biological Species Concept) from those that define species "vertically", i.e. through time (like the Evolutionary Species Concept). However, I have refrained from this because many species concepts have mixed or combined theoretical underpinnings. The Hennigian Species Concept, for example, contains reproductive isolation but also elements of cladistic theory. In the list below, rather than grouping the different concepts, I follow Mayden (1999) and Wilkins (2006b, 2009b[1]) and simply order them alphabetically. I either give direct quotations or short definitions based on the key references. Wilkins (2009b) highlights what he calls "'basic' or 'elemental' conceptions" (p. 193) from which the other species concepts are formed—these are the following: Agamospecies Concept and Biological, Ecological, Evolutionary, Genetic, Morphological and Taxonomic Species Concepts. Mayden (1997) also lists what he calls the Polythetic Species Concept (a cluster concept based on the covariance of characters). I do not include it here because it rather refers to the ontological status of species. I discuss these issues in Chap. 3. Many of the below concepts are very similar to each other and sometimes even synonymous. I give related names and/or synonymous or similar concepts, but again this is not to be viewed as a complete list; for a more detailed list of synonyms, see again Mayden (1997) and Wilkins (2006b, 2009b).

Most of the below species concepts are operational concepts for the identification of species taxa. In that sense, they are more species criteria than species concepts. The difference between true (ontological) species concepts (like the Evolutionary, the General Lineage and the Unified Species Concepts) and operational species identification concepts/criteria will be discussed in detail in Sect. 5.2.

The term Phylogenetic Species Concept is particularly ambiguous. It is applied to a number of different concepts that all have their roots, in one way or another, in finding the basic units of phylogenetic/cladistic analyses or at least in finding a species concept that is in accordance with the principles of phylogenetic systematics (cladistics). There are many different ways of naming the concepts subsumed under the name Phylogenetic Species Concept. I have chosen to apply this name to

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[1] Wilkins (2009b), in the main text, does present a classification (reproductive isolation, evolutionary, phylogenetic, ecological, asexual, and other conceptions) when listing authors and their concepts, but many of the concepts could just as well have been listed under a category different from the one in which they are included (the Hennigian concept in this list is a phylogenetic conception, but, as stated above, it is also a reproductive isolation concept). In his list of concepts at the end of the book, he renders them in alphabetical order.

two concepts (a diagnosability and a monophyly version[2]), but the Hennigian Species Concept as well as the Cladistic, Composite and Internodal Species Concepts are also rooted in cladistic theory. I have chosen not to use the term Autapomorphic Species Concept as different versions of the Phylogenetic Species Concept have been attached that name by different authors (see Wilkins 2009a, note 7 and pp. 213ff.; Wilkins still uses the term but points out its ambiguity in the literature). The Phylo-Phenetic Species Concept for prokaryotes is a combination of the diagnosability and monophyly versions of the Phylogenetic Species Concept on the one hand and the Genotypic Cluster and Phenetic Species Concepts on the other. The fact that only a small number of species concepts bear the adjective "phylogenetic" does not imply that other concepts are necessarily "un-phylogenetic", just as many (or even all) species concepts can claim to be as biological as the Biological Species Concept, and adherents of all species concepts would claim to work in an evolutionary framework so that their concepts are no less evolutionary than the Evolutionary Species Concept itself. Names are in many ways historically contingent.

Finally, a comment on the term concept itself. In the Introduction (Sect. 1.6), I have already mentioned Wilkins's (2011) distinction between concepts and conceptions. He holds that really there is only one real species concept, one that he calls the "generative concept*ion* [sic] of species", based upon "some power, a generative capacity, to make progeny resemble parents, and it seems to rely upon seeds" (p. 59). This notion goes back to the ancient Greeks and underlies all or most notions of species since (see also Wilkins 2009a and Chap. 2). What is listed here as species concepts are, according to Wilkins, rather species conceptions.[3] He also lists seven "'basic' species concepts: *agamospecies* (asexuals), *biospecies* (reproductively isolated sexual species), *ecospecies* (ecological niche occupiers), *evolutionary species* (evolving lineages), *genetic species* (common gene pool), *morphospecies* (species defined by their form, or phenotypes), and *taxonomic species* (whatever a taxonomist calls a species)" (p. 58). His final solution to the question of how many species concepts there really are is this: "There is *one* species concept. There are *two explanations* of why real species are species . . . : ecological adaptation and reproductive reach. There are *seven* distinct definitions of 'species', and *27* current variations and mixtures. And there are $n + 1$ definitions of 'species' in a room of n biologists" (p. 60). Two more noteworthy, although rather satirical, species concepts have been named by Ward Wheeler (2012, p. 53, footnote 1): the "*political* (designated by national boundaries) and *financial* (if there's money in it) species concepts", to which could be added a "conservation species concept" (assigning a population species rank to increase its conservation priority). While

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[2] This diagnosability/monophyly dichotomy is in accordance with Minelli's (2015) and Stamos's (2003, p. 269) evaluation of Phylogenetic Species Concepts, although Stamos subsumes Rosen's (1978, 1979) concept based on apomorphies under diagnosability rather than monophyly (whereas Minelli doesn't). See Sect. 5.6 for more.

[3] It is somewhat confusing that the single concept according to Wilkins is called generative concept*ion*.

these last three concepts may actually play a role in certain situations, they are obviously not scientific.

1. Agamospecies Concept

Definition/ specification:	An umbrella concept for asexual lineages and uniparental organisms that are combined into species based on morphological or genetic similarities. The first definition of agamospecies (according to Wilkins 2009a) is Turesson (1929, p. 333): "An apomict-population the constituents of which, for morphological, cytological or other reasons, are to be considered as having common origin".[4]
Key references:	Turesson (1929), Cain (1954), Eigen (1993)
Related names/ concepts:	Agamotaxon, microspecies, paraspecies,[5] pseudospecies, quasispecies

2. Biological Species Concept

Definition/ specification:	Interbreeding natural populations reproductively isolated from other such groups; all individuals that produce fertile offspring (actually or potentially—this varies among definitions).
Key references:	Dobzhansky (1935, 1937), Mayr (1940, 1942, 1963, 1982)
Related names/ concepts:	Genetic Species Concept, Hennigian Species Concept, Recognition Species Concept, Reproductive Competition Species Concept

Simpson (1961, pp. 148ff.) calls the Biological Species Concept "genetic species" concept (not to be confused with the Genetic Species Concept listed below).

3. Biosimilarity Species Concept

Definition/ specification:	"A species is a primarily horizontal, all the while dynamic, phenotypic similarity complex of organisms objectively and maximally delimited by causal relations, in the case of sexual organisms mainly interbreeding, ecological, ontogenetic, and possibly social and sociomorphic relations, and in the case of asexual organisms mainly ecological, possibly gene transfer, and possibly social (e. g., colony formation) relations." (Stamos 2003, p. 297)
Key references:	Stamos (2003)
Related names/ concepts:	This concept combines ontological issues about species (species as relations) with many species criteria from other species concepts. There are similarities with the Biological, Morphological and Ecological Species Concepts as well as

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[4] From the English abstract, the definition in the main text is in German.

[5] The term paraspecies is also used to denote paraphyletic species (Ackery and Vane-Wright 1984, quoted from Crisp and Chandler 1996, p. 816).

with the diagnosability version of the Phylogenetic Species Concept, among others.

This species concept is a very ambitious one and obviously an attempt at covering all organisms (sexual and asexual) while at the same time introducing a new approach to the ontology of species (species as relations). It is explicitly formulated in a theoretical framework that gives ontological priority to the horizontal over the vertical dimension of species and that views species concepts based on pattern as superior to those based on processes (e.g. certain modes of speciation). It is also one of the few modern species concepts that regard similarity as essential for the species category, not only operationally in the identification of species but also ontologically in their definition. It is probably fair to say, though, that it has been largely neglected by both biologists and philosophers of biology. Some of the issues integral to this concept (such as horizontal vs vertical species, species as relations and similarity as an important species criterion) are discussed in Sects. 1.4 and 3.5 and Chap. 6.

4. Cladistic Species Concept

Definition/ specification:	"set of organisms between two speciation events, or between a speciation event and one extinction event, or that are descended from a speciation event" (Ridley 1989, p. 3, italicized in the original)
Key references:	Ridley (1989)
Related names/ concepts:	Hennigian Species Concept, Internodal Species Concept

5. Cohesion Species Concept

Definition/ specification:	"the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (Templeton 1989, p. 12); "the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability" (Templeton 1989, p. 25)
Key references:	Templeton (1989)
Related names/ concepts:	–

Genetic and demographic exchangeability are the two different types of cohesion mechanisms. Genetic exchangeability is defined as "the factors that define the limits of spread of new genetic variants through *gene flow*" (Templeton 1989, p. 13). These factors are a compatible fertilization system (making reproduction possible), a compatible developmental system (making offspring viable and fertile) and lack of gene flow with other groups which preserves the genetic identity of species. Demographic exchangeability is defined as "the factors that define the fundamental niche and the limits of spread of new genetic variants through *genetic drift* and *natural selection*" (Templeton 1989, p. 13). Complete demographic exchangeability occurs “when all individuals in a population display exactly the same ranges and abilities of tolerance to all relevant ecological variables” (Templeton 1989, p. 15). The Cohesion Species Concept covers both asexual and sexual taxa across the whole spectrum; in the former, only demographic exchangeability determines species status and species boundaries (genetic exchangeability does not apply), whereas in the latter both genetic and demographic exchangeability are relevant (to varying degrees).

6. Compilospecies Concept

Definition/ specification:	“A compilospecies is genetically aggressive, plundering related species of their heredities, and in some cases it may completely assimilate a species, causing it to become extinct” (Harlan and De Wet 1963, p. 499). This describes what is today called introgressive hybridization. Wilkins (2009b, p. 193) calls this concept a “partial” species conception.
Key references:	Harlan and De Wet (1963)
Related names/ concepts:	Nothospecies Concept

7. Differential Fitness Species Concept

Definition/ specification:	“groups of individuals that are reciprocally characterized by features that would have negative fitness effects in other groups and that cannot be regularly exchanged between groups upon contact” (Hausdorf 2011, p. 923, 927)
Key references:	Hausdorf (2011)
Related names/ concepts:	Biological Species Concept, Cohesion Species Concept, Genetic Species Concept

8. Ecological Species Concept

Definition/ specification:	“a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range” (Van Valen 1976, p. 233)
Key references:	Van Valen (1976)
Related names/ concepts:	Cohesion Species Concept, Evolutionary Species Concept, General Lineage Species Concept

It should be noted that the Ecological Species Concept is not just about ecological niches. The second (or rather, first) criterion is that species are lineages; the concept is therefore genealogically based as well (Ereshefsky 2001, p. 88). Contrary to that, Stamos (2003, p. 146) holds that, because Van Valen “allows for more than one lineage in niche occupation, as well as polyphyly or multiple origins . . . his species concept is fundamentally a class concept”. However, upon reading Van Valen (1976), it seems to me that these points are not central to his species concept; they are raised when discussing symbiotic entities such as lichens or corals and their endosymbiotic algae, and the question of whether these entities should be considered species.

9. Evolutionar(il)y Significant Unit (ESU)

Definition/ specification:	A distinct portion of a species' evolutionary legacy considered worthy of particular protection/conservation; the distinction of intraspecific portion (populations) vs separate species is not always made clear; defined, depending on authors, by isolation, monophyly, genetic differentiation, genetic and ecological exchangeability.[6]
Key references:	Ryder (1986), Waples (1991), Moritz (1994), Crandall et al. (2000)
Related names/ concepts:	Depending on the concrete definition of ESUs: Biological Species Concept, Evolutionary Species Concept, Phylogenetic Species Concept (monophyly version), Cohesion Species Concept

This concept is mostly not used as an explicit species concept but rather as an attempt at a more objective alternative to the subspecies in a conservation context (see the seminal publication by Ryder 1986 and Sect. 5.9). But because the distinction between intra- and interspecific application is not always clear, the ESU concept is sometimes listed as a species concept as well (e.g., by Mayden and Wilkins).

10. Evolutionary Species Concept

Definition/ specification:	Species are ancestor-descendant lineages that evolve separately from other such lineages and have their own evolutionary tendencies and historical fate.
Key references:	Simpson (1951, 1961), Wiley (1978), Wiley and Mayden (2000a)
Related names/ concepts:	General Lineage Species Concept, Unified Species Concept

In most definitions, the ancestor-descendant lineages are called population lineages, but Wiley and Mayden (2000a) have dropped the reference to populations to include asexual taxa in the Evolutionary Species Concept because asexuals do not form populations (at least not in the way that sexual organisms do).

11. Genealogical Species Concept

Definition/ specification:	"basal, exclusive groups of organisms, where exclusive groups are ones whose members are all more closely related to each other than to any organisms outside the group" (Baum and Shaw 1995, p. 289); "There must be a taxon whose relationships with

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[6] Crandall et al. (2000) explicitly refer to Templeton (1989) but use the term ecological exchangeability (rather than demographic exchangeability). They also refer to Templeton (1994) in which ecological and demographic exchangeability seem to be used synonymously.

	other taxa are predominantly divergent but whose parts (the organisms ascribable to the taxon) are related to each other by a predominantly reticulate genealogy. We refer to this entity as the 'genealogical species (. . .)'" (Baum and Shaw 1995, p. 291).
Key references:	Baum and Shaw (1995), Baum (1998)
Related names/ concepts:	Phylogenetic Species Concepts, Genealogical Concordance Species Concept

This species concept is another one from the family of, broadly speaking, Phylogenetic Species Concepts. Baum and Shaw (1995, p. 291, footnote 5) explicitly use the adjective "genealogical" to distinguish their concept from the variety of concepts and subconcepts called Phylogenetic Species Concepts.

The term exclusivity is essential to this concept. As can be seen from the quote above, it refers to groups of organisms that are all more closely related to each other than to any organism outside the group (see also Baum 1992, 1998). It is important to note that exclusivity is not the same as monophyly. While there are different definitions of monophyly, the term usually refers to a group that comprises all and only descendants of an ancestral species. Whether the ancestral species is included in the group is where some definitions differ, but in the present context, this is irrelevant. Exclusivity and monophyly only converge if the phylogeny is purely divergent (only branching events, no merging of lineages, i.e. no hybridization or reticulation). In the case of reticulation/hybridization, the offspring of that event is part of the monophyletic group because they are also descendants of the most recent common ancestor of that group. However, they are more closely related to the parental species that is not part of that monophylum. Including the offspring in the monophylum (thus violating the condition for exclusivity) is called "network gain", and such a group is said to be "epiphyletic" by Wheeler (2014).[7] Excluding these offspring (violating the condition for monophyly), Wheeler calls "network loss", and the group is said to be "periphyletic"[8] (Fig. 4.1). Since Baum and Shaw (1995) view the species rank at the interface of reticulating and divergent relationships (the tokogeny/phylogeny divide sensu Hennig), the preference of exclusivity makes perfect sense, because monophyly is not applicable to reticulating systems. It also implies that the Genealogical Species Concept is only applicable to sexual taxa because asexual taxa do not have reticulating relationships. Graybeal (1995) suggested to distinguish between interbreeding species that meet the condition of exclusivity ("exclusive species") and interbreeding species that do not ("ferespecies", from Latin *fere* = almost). While the distinction is relevant, the suggested terminology has not caught on.

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[7] This is Ward Wheeler, not Quentin Wheeler (the proponent of a diagnosability version of the Phylogenetic Species Concept).

[8] For a group that shows both a network gain and a network loss after more than one reticulation event, Wheeler suggests the term "anaphyletic".

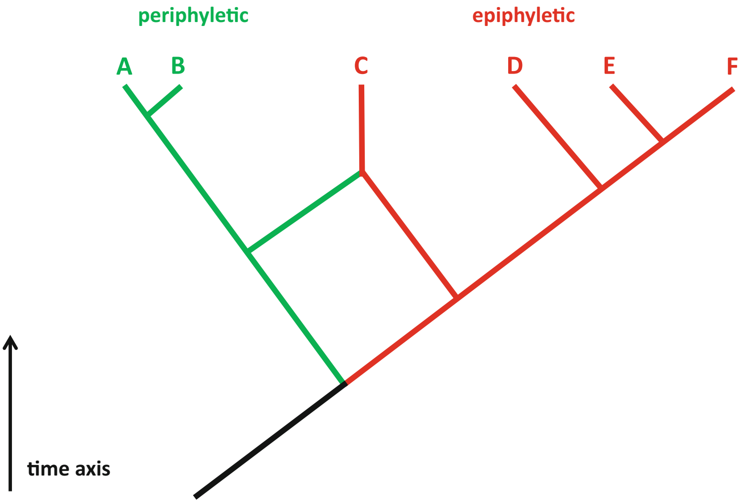

Fig. 4.1 Group names in a phylogeny with reticulation. A–F are operational taxonomic units with C being of hybrid origin. The *green group* is not monophyletic because C, although going back to its common ancestor (via the green parent of the hybridization event), is not included ("periphyly" through "network loss"). The *red group*, on the other hand, is monophyletic (it contains all and only descendants of the most recent common ancestor shared by species C–F), but it is not exclusive because C is more closely related to its green parent than to D, E and F ("epiphyly" through "network gain")

The term "basal" in their species definition refers to the demand that species be the least inclusive exclusive group, i.e. "they cannot contain nested within them any other exclusive groups" (Baum and Shaw 1995, p. 291).

A very interesting and important consequence of the Genealogical Species Concept is that it explicitly allows (and indeed expects) species boundaries to be fuzzy. Relatedness (as in "more closely related" in the species concept definition above) is defined by Baum and Shaw (1995) not in terms of recency of a common organismic ancestor but instead in terms of gene coalescence. Very briefly, this is to account for reticulation due to recombination that goes undetected when focusing on the level of the organism. Accordingly, in terms of coalescence, exclusivity is defined as follows: "A group of organisms is exclusive if their genes coalesce more recently within the group than between any member of the group and any organism outside the group" (Baum and Shaw 1995, p. 296). Even if the majority of genes result in concordant topologies, some genes will produce non-concordant topologies,[9] and consequently species will have fuzzy boundaries. This is not due to the concept itself but because "species have inherently fuzzy boundaries" (p. 301), and

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[9] In general, gene trees (even if correctly inferred) will vary, and they can also be discordant with the organismal phylogeny of the carriers of those genes (species trees) (see Zachos 2009 for a review and further references).

this fuzziness becomes apparent when the species concept is applied to real organisms. My personal opinion is that concepts that capture inherently fuzzy boundaries are better representations of the nature of species taxa than those that don't. Fuzzy boundaries, therefore, are a recurrent theme in this book.

Baum and Shaw (1995, p. 300) see species primarily as restricted to one slice of time (horizontal species), making species "analogous to the instantaneous morphologies (semaphoronts) that make up the development pathway of organisms (Hennig, 1966)". The issue of horizontal vs vertical species is discussed in Sect. 1.4, where it is argued that there is and cannot be an ontological difference between the horizontal (or synchronic) and the vertical (or diachronic) dimension of a species.

12. Genealogical Concordance Species Concept

Definition/ specification:	"population subdivisions concordantly identified by multiple independent genetic traits should constitute the population units worthy of recognition as phylogenetic taxa" (Avise and Ball 1990, p. 52).
Key references:	Avise and Ball (1990)
Related names/ concepts:	Biological Species Concept, Phylogenetic Species Concepts

While still granting the Biological Species Concept theoretical primacy, Avise and Ball's concordance approach explicitly aims at reconciling the Biological with Phylogenetic Species Concepts. They give priority to intrinsic (genetic) over geographical (extrinsic) reproductive barriers in determining species because the former are less likely to break down and therefore also less likely to result in ephemeral entities.

13. General Lineage Species Concept

Definition/ specification:	"segments of population level evolutionary lineages" (de Queiroz 1998, p. 60; see also definition of the Unified Species Concept below)
Key references:	de Queiroz (1998, 1999)
Related names/ concepts:	Evolutionary Species Concept, Unified Species Concept

This is an attempt—similar to that based on the Unified Species Concept and Mayden's (1997) interpretation of the Evolutionary Species Concept (see Sect. 5.2)—at finding the common denominator of all species concepts. The solution is that all species concepts consider species as lineages of groups of organisms or segments thereof. Populations are defined here as an organizational level above that of the organism, not as a reproductive community of sexual organisms. The General Lineage Species Concept is therefore also meant to apply to asexual taxa.

14. Genetic Species Concept

Definition/ specification:	"a group of genetically compatible interbreeding natural populations that is genetically isolated from other such groups

. . . genetic isolation and protection of the integrity of the two respective gene pools” (Baker and Bradley 2006, p. 645).

Key references: Simpson (1943), Dobzhansky (1950),[10] Baker and Bradley (2006)

Related names/concepts: Biological Species Concept, Differential Fitness Species Concept

Genetic isolation is different from the reproductive isolation of the Biological Species Concept in that it allows occasional interbreeding as long as the integrity of the two gene pools is not broken up. While being the most prominent proponent of the Biological Species Concept, Ernst Mayr has also said that the species is “a genetic unit consisting of a large, intercommunicating gene pool” (Mayr 1969, p. 26) which is basically a definition of the Genetic Species Concept. Mayr, in later publications, has increasingly emphasized that species are harmonious gene pools that protect themselves against harmful gene flow from other integrated gene pools, showing the similarity of his views with the Genetic Species Concept.

15. Genic Species Concept

Definition/specification: “species are groups that are differentially adapted and, upon contact, are not able to share genes controlling these adaptive characters, by direct exchanges or through intermediate hybrid populations. These groups may or may not be differentiated elsewhere in the genome” (Wu 2001a, p. 855).

Key references: Wu (2001a, b)

Related names/concepts: Biological Species Concept, Differential Fitness Species Concept, Genetic Species Concept

Wu (2001a) is a target review on speciation in an issue of the *Journal of Evolutionary Biology* which is followed by short comments and criticisms by different authors. Wu (2001b) is the reply to these criticisms. He views his genic view of species as an alternative to the Biological Species Concept, putting more emphasis on the specific parts of the genome involved in adaptation and divergence rather than the whole genome as a single unit. As expected, this (i.e. the redefinition of species) has not remained uncriticized (e.g. Orr 2001 and Rundle et al. 2001), but the fact that different regions of the genome show different rates of gene flow has been well established by now (e.g. Poelstra et al. 2014).

16. Genotypic Cluster Species Concept

Definition/specification: “distinguishable groups of individuals that have few or no intermediates when in contact”; these clusters are identified

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[10] Both Mayden (1997) and Wilkins (2006b, 2009b) cite Dobzhansky (1950) as a key reference for the Genetic Species Concept, but both give an incorrect citation: The paper “Mendelian populations and their evolution” was not published in volume 74, pp. 312–321, of the American Naturalist, but in volume 84, pp. 401–418. The paper in volume 74 (1940) is Dobzhansky’s “Speciation as a stage in evolutionary divergence”.

	using morphology and genetics, and genetic clusters “are recognized by a deficit of intermediates, both at single loci (heterozygote deficits) and at multiple loci (strong correlations or disequilibria between loci that are divergent between clusters)” (Mallet 1995, p. 296).
Key references:	Mallet (1995)
Related names/ concepts:	Biological Species Concept, Genealogical Concordance Species Concept, Genetic Species Concept, Morphological Species Concept, Phenetic Species Concept, diagnosability version of the Phylogenetic Species Concept, and others

17. Hennigian Species Concept

Definition/ specification:	“Species are reproductively isolated natural populations or groups of natural populations. They originate via the dissolution of the stem species in a speciation event and cease to exist either through extinction or speciation” (Meier and Willmann 2000a, p. 31, based on Willmann 1985 and Willmann 1986).
Key references:	Hennig (1950, 1966), Meier and Willmann (2000a)
Related names/ concepts:	Biological Species Concept, Cladistic Species Concept, Internodal Species Concept

The Hennigian Species Concept is very much the Biological Species Concept extended through time. It is based on the Hennigian Convention (necessary dissolution of the stem species in a speciation event) and reproductive isolation. However, Meier and Willmann (2000a) make it clear that they refer to *absolute* reproductive isolation (no fertile hybrids at all), because they hold that only this makes objective species delimitation possible: if not only absolute reproductive isolation is accepted as the arbiter, then one has to agree on a level of allowed degree of hybridization, which is “entirely arbitrary” (Meier and Willmann 2000a, p. 40). They only apply their species concept to sexual taxa; asexuals they call agamotaxa instead to underline their different ontological status.

18. Internodal Species Concept

Definition/ specification:	“individual organisms are conspecific in virtue of their common membership of a part of the genealogical network between two permanent splitting events or between a permanent split and an extinction event” (Kornet 1993, p. 408).
Key references:	Kornet (1993)
Related names/ concepts:	Cladistic Species Concept, Composite Species Concept, Hennigian Species Concept

Wilkins (2006b, 2009b) also lists the Composite Species Concept and gives Kornet and McAllister (1993) as the reference, while Mayden (1997) included Kornet and McAllister (1993) in the references for the Internodal Species Concept. For all biologically relevant purposes, both names refer to the same species concept.

What Kornet (1993) introduces as the internodal species concept is basically a version of the cladistic species concept in formal set theoretical terms whose core is what she calls the conspecificity relation INT. Kornet emphasizes that speciation depends on the permanent splitting of lineages, which can only be evaluated in hindsight. She shares the view that species can only safely be delimited retrospectively with Sober (1984) and O'Hara (1993). Strictly speaking, and Kornet is explicit about this, correct species delimitation can only be made after the extinction of the whole genealogical network (i.e. the complex of lineages under scrutiny) because only then it is certain that no parts of the network will ever reunite (hybridize).[11]

19. Least Inclusive Taxonomic Unit (LITU)

Definition/ specification:	LITUs are, like all other taxa in a phylogenetic system, "named monophyletic groups which are identified by unique shared similarities (apomorphies). … [LITUs are] at present not further subdivided. …LITUs are statements about the current state of knowledge (or lack thereof) without implying that they have no internal nested structure; we simply do not know if a given LITU consists of several monophyletic groups or not" (Pleijel and Rouse 2000, p. 629).
Key references:	Pleijel (1999), Pleijel and Rouse (2000)
Related names/ concepts:	Phylogenetic Species Concept (those versions based on monophyly/apomorphies)

Pleijel (1999) gives a worked-out example; Pleijel and Rouse (2000) formally introduce the LITU concept. Since the existence of the species category is rejected, LITUs are not really a species concept; they are meant to replace the species category as the operational taxonomic unit in phylogenetics. The underlying idea is that all nested levels of monophyla in a phylogenetic system are equivalent. The species category is rejected as a real entity (species category nominalism). Like higher taxa, LITUs are uninomials, but unlike them, they are written in lower-case letters. Pleijel and Rouse's (2000) views are similar to those of Mishler (1999) (see Sect. 3.6). They define names strictly phylogenetically, without reference to Linnaean ranks or type specimens and in accordance with demands for a phylogenetic nomenclature and the *PhyloCode* (e.g. de Queiroz and Gauthier 1992, 1994, Cantino et al. 1999, Dayrat et al. 2008 and Cantino and de Queiroz 2010).

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[11] Stamos (2003, footnote 1, p. 187f.) rejects this as teleological because it is a "backwards causation". This, however, is a very feeble argument as it seems to me to be very clear that the retrospective approach in species delimitation is only "backwards diagnosis", not causation, and aims at avoiding the assignment of species status to ephemeral units. It is not any more teleological than to say that when someone has been shot, whether the perpetrator will be prosecuted for homicide or grievous bodily harm can only be decided after the victim has either died or recovered.

20. Morphological Species Concept

Definition/ specification:	“Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means” (Cronquist 1978; quoted from Wilkins 2009b, p. 157).
Key references:	This has been the most widely spread species concept in taxonomic practice from at least Aristotle through Linnaeus to the present. A more recent reference is Cronquist (1978).
Related names/ concepts:	Classical species, Linnaean species, Phenetic Species Concept, Phylogenetic Species Concept (diagnosability version)

Wilkins emphasizes that the Morphological Species Concept, contrary to the received view of the Essentialism Story, “was never anything more than a diagnostic account of species” (Wilkins 2009b, p. 197, see also Wilkins 2009a). Needless to say, in the above quote from Cronquist species recognition hinges on what is considered “ordinary means” (today or very soon it will include genomic data, back in 1978 it didn’t).

21. Non-dimensional Species Concept(s)

Definition/ specification:	Species delimitation with restricted or no spatial and temporal dimension (i.e. in sympatry and synchrony).
Key references:	for the Biological Species Concept, e.g. Mayr (1940, 1942, 1963)
Related names/ concepts:	The most prominent non-dimensional concept is the Biological Species Concept, but others are also largely non-dimensional, at least in practice (e.g. the Genetic Species Concept and the Phenetic Species Concept).

This is rather a group of species concepts (a classification of species concepts) than a single concept in itself. I have included it because one often comes across this term in discussions of species concepts. It is an operational concept, an artificial limitation to sympatry and synchrony for practical or pragmatic reasons (although species do of course have spatial and temporal extension beyond the one accounted for by a non-dimensional approach).

22. Nothospecies Concept

Definition/ specification:	Species formed through hybridization of two parental species, in plants often by polyploidy.
Key references:	Wagner (1983)
Related names/ concepts:	Hybrid or hybridogenic species, Compilospecies Concept

Wilkins (2009b, p. 193) calls this concept a “partial” species conception.

23. Phenetic Species Concept

Definition/ specification:	“the species level is that at which distinct phenetic clusters can be observed” (Sneath 1976, p. 437); phenetic species are based on overall similarity and form clusters in character space: “The

phenetic species concept advocated by the numerical taxonomists is based on the numerical evaluation of the boundaries of populations in a character hyperspace" (Sokal 1973, p. 361, italics of the original removed).

Key references: Sokal and Sneath (1963), Sokal (1973), Sneath (1976)

Related names/concepts: Since the Phenetic Species Concept is so general, it shows overlap with many other concepts, perhaps most notably with the Morphological Species Concept and the Genotypic Cluster Concept. Numerical taxonomy (Sokal and Sneath 1963) is also closely related to the ideas of the Phenetic Species Concept.

Wilkins (2006b, 2009b) regards the Phenetic Species Concept as a family resemblance concept (see Sect. 3.3) with clusters of characters that covary statistically.

24. Phylogenetic Species Concept (Diagnosability Version)

Definition/specification: "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983, p. 170, original in italics);
"the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states" (Wheeler and Platnick 2000a, p. 58).

Key references: Eldredge and Cracraft (1980), Nelson and Platnick (1981), Cracraft (1983), Nixon and Wheeler (1990), Wheeler and Platnick (2000a)

Related names/concepts: Genotypic Cluster Species Concept, Morphological Species Concept, Phenetic Species Concept

The definition by Cracraft is a bit ambiguous because it does not become clear that it refers to the population level. If taken literally, family groups with a de novo mutation would qualify as phylogenetic species. This is not what Cracraft meant, and consequently he has modified his definition, replacing "smallest cluster of individuals" with "smallest population or group of populations" (Cracraft 1997, p. 329, see also p. 330).

Diagnosability does not per se mean that these characters are apomorphic (see monophyly version of the Phylogenetic Species Concept). In fact, it does not even necessarily mean that different characters are fixed in different species. In taxonomic practice, the diagnosability concept can be very similar to the Phenetic Species Concept if two populations are considered distinct species when they show no overlap in character space (i.e. are 100 % diagnosable). This is often done by means of discriminant or principal component analyses based on morphometric data (for a recent example in mammals—which led to a huge increase in species numbers—see Groves and Grubb (2011)) but can be done just as well with allele frequency data. Imagine two populations 1 and 2 and two alleles A and B at a high number of marker loci. Population 1 harbours individuals that only carry A alleles except for a single or very few individuals that carry one B at one of the loci such that in population 1 as a whole A and B are present at all loci. Population 2 is the exact complementary (all Bs except for single A alleles). A cluster analysis will yield two distinct, non-overlapping clouds without a single individual being assigned to the "wrong" population. The two populations will thus be diagnosably distinct, and every single individual can be unambiguously identified as belonging to one of the two populations which are then considered two distinct species. However, both populations show the same alleles/character states at each locus (A and B); none of them is fixed for even a single diagnostic allele. This I call *quantitative or statistical diagnosability* as opposed to *qualitative diagnosability* (fixed differences for at least one character). In the latter, a single character state (or each of many such character states) makes the two populations diagnosable, while in the former, diagnosability is a statistical concept or property. Quantitative diagnosability is in accordance with Nelson and Platnick's (1981, p. 12) view that species need not have a single unique trait, just a unique diagnosable combination of characters. Qualitative diagnosability is therefore based on a difference in kind, while quantitative diagnosability is rather based on a difference in degree.

25. Phylogenetic Species Concept (monophyly version)

Definition/ specification:	"A species is the least inclusive taxon recognized in a formal phylogenetic classification. As with all hierarchical levels of taxa in such a classification, organisms are grouped into species because of evidence of monophyly. Taxa are ranked as species rather than at some higher level because they are the smallest monophyletic groups deemed worthy of formal recognition, because of the amount of support for their monophyly and/or because of their importance in biological processes operating on the lineage in question" (Mishler and Theriot 2000a, p. 46f).
Key references:	Rosen (1978, 1979), Mishler and Donoghue (1982), Mishler (1985), Donoghue (1985), Mishler and Brandon (1987), Mishler and Theriot (2000a)
Related names/ concepts:	Cladistic Species Concept; Platnick and Wheeler (2000, p. 186) suggest the terms Autapomorphic Species Concept or Monophyletic Species Concept for this phylospecies version (but see comment above on the ambiguous use of the term Autapomorphic Species Concept in the literature).

Whether or not the concept of monophyly is applicable to the lowest taxonomic levels (including the species level) is a contentious issue (see Sect. 5.6.1).

Mayden (1997) distinguishes a third version of the Phylogenetic Species Concept, one based on diagnosability *and* monophyly. The key reference he gives is McKitrick and Zink (1988) who use the diagnosability concept of Cracraft (1983) and add monophyly as an additional condition for species status: "… lead us to advocate a phylogenetic species concept (PSC) (sensu Cracraft 1983), in which all taxa are monophyletic, diagnosable clusters of individuals and species are the smallest diagnosable clusters" (McKitrick and Zink 1988, p. 1). I have not included this third version for the following reasons. Strictly speaking, monophyly and diagnosability/apomorphies are independent, at least in an ontological sense: monophyly is the status of being a complete community of descent comprising an ancestor and all of its descendants (and only those) regardless of the presence of apomorphies. Apomorphies—or more precisely, the character states hypothesized to be apomorphic based on a phylogenetic analysis—are used to *identify* monophyla, but they do not define them. Monophyly is a historical relation, not the presence of any character state. If populations split up in a hierarchical manner, a pattern of monophyly emerges even if not a single change in character state is involved. However, unless one directly observes the history of population sundering (e.g. in a laboratory experiment where one separates groups of fruit flies or Petri dishes of cultivated bacteria), this history can only be reconstructed with the help of apomorphies. For all practical purposes, therefore, monophyla and apomorphies go together, and monophyla will be diagnosable through these apomorphies (and perhaps additionally some plesiomorphies as well). Indeed, Rosen's (1978, 1979) species concept defines species on the basis of their *diagnostic apomorphies*, neatly summing up that (inferred) monophyly includes diagnosability, whereas diagnosability does not necessarily entail monophyly.[12] There is, however, one restriction to this: if phyletic or anagenetic speciation is allowed (as in the diagnosability version of the Phylogenetic Species Concept *sensu* Wheeler and Platnick (2000a)), then the fixation of an apomorphy (or any other trait) will lead to a diagnosable "chronospecies", not to a monophylum of branching lineages (but a continuous populational lineage may of course be said to comprise all descendants of the preceding "chronospecies").

26. Phylo-Phenetic Species Concept

Definition/ specification:	"a monophyletic and genomically coherent cluster of individual organisms that shows a high degree of overall similarity with respect to many independent characteristics, and is diagnosable by a discriminative phenotypic property" (Rosselló-Mora and Amann 2001, p. 59; italicized in the original)
Key references:	Rosselló-Mora and Amann (2001)
Related names/ concepts:	Phylogenetic Species Concept (diagnosability version), Phylogenetic Species Concept (monophyly version), Genotypic Cluster Species Concept, Phenetic Species Concept

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[12] One might argue that the last paragraph has been written in the spirit of the phylogenetic school called process cladism and that pattern cladists would refrain from historical interpretations (common ancestry) as long as possible and instead only analyze the distribution of different character states. Cladograms would then not be phylogenetic trees but primarily "synapomorphy schemes" (Nelson and Platnick 1981, p. 141). See Sect. 5.6 for a short description of process and pattern cladism with respect to Phylogenetic Species Concepts.

The Phylo-Phenetic Species Concept was specifically introduced for prokaryotic organisms (see Sect. 5.7). It combines elements of the Phylogenetic Species Concept (both the diagnosability and the monophyly version) with clustering concepts like the Genotypic Species Concept and the Phenetic Species Concept.

27. Pragmatic Species Concept

Definition/ specification:	"A species is a cluster of organisms which passed a threshold of evolutionary divergence. Divergence is determined by one or several operational criteria described by an adequate numerics. A single conclusive operational criterion is sufficient. Conflicts between operational criteria require an evolutionary explanation. Thresholds for each operational criterion are fixed by consensus among the experts of a discipline under the principle of avoiding over-splitting. Clusters must not be the expression of intraspecific polymorphism." (Seifert 2014, p. 89)
Key references:	Seifert (2014)
Related names/ concepts:	Morphological Species Concept, Phenetic Species Concept

This concept is a recent attempt at a standardized operational pattern-based concept. While it might contribute to more repeatable taxonomic practice (which is important!), it does not fully solve the problem of among-taxonomist differences in deciding what exactly is meant by adequate numerics and where thresholds are to be drawn.

28. Recognition Species Concept

Definition/ specification:	"...regard a species as that most inclusive population of individual biparental organisms which share a common fertilization system" (Paterson 1985, p. 25, original in italics, quoted from Wilkins 2009b, p. 141); Paterson's common fertilization system is based on the recognition of reproductive mates, or a "specific mate recognition system".
Key references:	Paterson (1985)
Related names/ concepts:	Biological Species Concept, Genetic Species Concept

Paterson's species concept changed over time. While in the beginning he focused on what he called a *specific mate recognition system* (SMRS) which referred to finding an appropriate mating partner (incl. chemical communication, i.e. no conscious choice necessary or even meant), he later modified this concept when he realized that among plants (particularly orchids) different taxa considered to be species share the same SMRS. This is why in the above definition, SMRS are not mentioned but have been replaced by "a common fertilization system" of which the SMRS is just a subset. A fertilization system is defined as comprising "all characters that contribute to the achievement of fertilization. These characters are diverse and include such characters in the mating partners as the design features of the gametes, those determining synchrony in the achievement of reproductive condition, the coadapted signals and receivers of mating partners, and their coadapted organs of gamete delivery and reception" (Paterson 1988, p. 69; quoted from Stamos 2003, p 198, footnote 14). Stamos (ibidem) rightly asks if the concept shouldn't be called fertilization concept (now that the SMRS is not what distinguishes species anymore), but because the concept is still widely known as the Recognition Species Concept (and Paterson also keeps calling it that), I have adopted that name as well. Although there are differences, the close relationship with the Biological Species Concept is obvious, but the recognition concept has not nearly been as successful and has often been considered to be just a different version of Mayr's and Dobzhansky's biological concept.

29. Reproductive Competition Species Concept

Definition/ specification:	"Species . . . are the most extensive units in the natural economy such that reproductive competition occurs among their parts" (Ghiselin 1974a, p. 538, partly in italics in the original).
Key references:	Ghiselin (1974a, b, 1997)
Related names/ concepts:	Biological Species Concept, "'bioeconomic' version of the biological species definition" (Ghiselin 1997, p. 110), hypermodern species

This definition is typical of Ghiselin's analogy of species in biology and firms in economies (see Chap. 9 of Ghiselin 1997 for a short description of that analogy). It should also be noted that Ghiselin is a proponent of the Biological Species Concept and that he regards the bioeconomic concept not as an alternative concept, but rather as an alternative formulation or explication of it.

30. Successional Species Concept

Definition/ specification:	"Arbitrary anagenetic stages in morphological forms, mainly in the paleontological record" (Wilkins 2006b, 2009b, p. 198).
Key references:	George (1956), Simpson (1961)
Related names/ concepts:	Chronospecies, paleospecies

While Simpson (1951, 1961) advocated the Evolutionary Species Concept, in practice he argued for the subdivision of single lineages into morphological chronospecies. This kind of phyletic or anagenetic speciation is also allowed for by at least some adherents of the diagnosability version of the Phylogenetic Species Concept (see Wheeler and Platnick 2000a).

31. Taxonomic Species Concept

Definition/ specification:	". . .a species consists of all the specimens which are, or would be, considered by a particular taxonomist to be members of a single kind as shown by the evidence of the assumption that they are as alike as their offspring or their hereditary relatives within a few generations" (Blackwelder 1967, p. 164).
Key references:	Regan (1926), Blackwelder (1967)

Related names/ concepts:	Cynical Species Concept, Morphological Species Concept, Phenetic Species Concept

The famous name “Cynical Species Concept” goes back to Kitcher (1984, p. 308): “The most accurate definition of ‘species’ is the cynic’s. Species are those groups or organisms which are recognized as species by competent taxonomists. Competent taxonomists, of course, are those who can recognize the true species”.

32. Unified Species Concept

Definition/ specification:	“A unified species concept can be achieved by interpreting the common fundamental idea of being a separately evolving lineage segment as the only necessary property of species” (de Queiroz 2005b, p. 196).
Key references:	de Queiroz (2005b, 2007)
Related names/ concepts:	Evolutionary Species Concept, General Lineage Species Concept (the latter is practically identical to the Unified Species Concept)

Like the General Lineage Species Concept, the Unified Species Concept aims at the common denominator of all species concepts that de Queiroz identifies as a population lineage: “Virtually all contemporary species concepts equate species with populations or population lineages—or more accurately, with segments of population level lineages” (de Queiroz 2005b, p. 198). Elsewhere he calls this common denominator a “separately evolving metapopulation lineage” or segments of such lineages (de Queiroz 2007). I have included the Unified Species Concept here in addition to the General Lineage Concept because it is sometimes cited instead or in addition to it and because the independence of species lineages from one another (“separately evolving”) is emphasized more explicitly by de Queiroz here than in his publications on the General Lineage Species Concept.

Chapter 5
Species Concepts and Beyond: Selected Topics Relating to the Species Problem

This chapter is best viewed as an attempt at going a little bit deeper into various aspects of the species problem while at the same time serving the overall aim of this book: to provide biologists with a distillation, as it were, of the species debate(s). Therefore, none of the subchapters claim to present an exhaustive discussion of its topic or species concept. Rather, they are best viewed as short commentary sections. As in many other sections of this book, the reader will see that often seemingly different views actually have a lot in common. I am not denying that there are important differences between various species concepts, but sometimes they are exaggerated, and the theoretical solution to the species problem (or at least an important part of it) in the form of a hierarchy of species concepts is proof that there is enough common ground for reconciliation. Cracraft (2000, p. 7) was right when he remarked on the similarity of species concepts saying “Similarities: all else is rhetoric” and “A student of species concepts must be able to sort through the rhetoric, unless, of course, the goal is to use it for one’s own gain”. In this book I argue that all species concepts are based on biological realities. Thus, none of them can simply be wrong. Some may be more general or more consistent with research results in different disciplines, and one or several may be superior to others (as indeed, I think, is the case with the Evolutionary Species Concept or General Lineage/Unified Species Concept), but all are real in the sense that they capture biological phenomena. This should be kept in mind because as Stamos (2003, p. 355) put it: “And indeed there is ‘something natural and something beautiful’ in each and every species concept, which taken together in their diversity reveal a conceptual world as rich and as breathtaking, in its own way, as anything to be found in the biological world. And if symbiosis in the biological world is truly a source of evolutionary innovation, there is no reason why it cannot also be so in the conceptual world of theories. All the more reason, then, to value rather than slash and burn the diversity of solutions to the species problem, for out of that diversity endosymbiotic innovations may be born”. This is not to say, and Stamos also adds this, that there are not better and less good solutions, but it is worth remembering when species debates become heated.

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5.1 Agamospecies: Are Sexual and Asexual Species the Same?

The question in the headline of this subchapter is often formulated as "Do asexual organisms form species?", and a common answer is that asexuals are species-less, but this is somewhat ambiguous. First, asexuals do have species names as T species in taxonomy. Second, they certainly form lineages and give rise to new taxa or lineages. Denying these taxa the name species presupposes that the term species is reserved for sexual organisms, so it is really better to ask more neutrally whether what is called species in sexuals and asexuals is the same or a different kind of entity.

The term agamospecies was coined by Turesson (1929) and gained wide acceptance through Cain (1954) (see Wilkins 2009b). Cain accepts this concept as a consequence of the fact that the Biological Species Concept is not applicable to asexual taxa. To him, the delimitation of agamospecies is the same as for morphospecies. The original definition of Turesson is "An apomict-population the constituents of which, for morphological, cytological or other reasons, are to be considered as having a common origin" (Turesson 1929, p. 333). Instead of agamospecies other terms have been used (agamotaxa, e.g. Meier and Willmann 2000a; agameon, Camp and Gilly 1943; pseudospecies, Ghiselin 1987b; binomial, Camp 1951[1]), but it is always the lack of reproductive relationships and genetic exchange that triggers the need for a different term.

A related conception for viruses is the quasispecies of Manfred Eigen and colleagues. Quasispecies are regions in sequence space at the centre of which is the ancestral sequence to which all other sequences coalesce; they are "self-sustaining population[s] of sequences that reproduce themselves imperfectly but well enough to retain a collective identity over time" (Eigen 1993, quoted from Wilkins 2009b, p. 163[2]). The quasispecies contains two aspects that can almost be called universal to all species concepts: a common ancestor and the existence as an independent lineage through time.

That this is a difficult and important issue can also be seen from the fact that some authors have changed their minds, or are equivocal about it in their published works. For example, Wiley and Mayden (2000a) have dropped the word population from the definition of the Evolutionary Species Concept to include asexuals, but at the same time, they admit to ontological differences between the two (Wiley and Mayden 2000c).[3] And there is little doubt that there are fundamental differences between sexual and asexual organisms. Genetic exchange through reproduction and

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[1] These last two references I owe to Wilkins (2009b, p. 164).

[2] Eigen (1993) is a nontechnical account of the molecular quasispecies. The concept was first published by Eigen et al. (1988, 1989), but these are formal mathematical discussions in the framework of physical chemistry and not easily accessible to most biologists (myself included).

[3] There are claims that Ernst Mayr, in an ecological formulation of his Biological Species Concept (Mayr 1982, p. 273), also for a time allowed asexuals to form true species (Ereshefsky 2001,

the concomitant reticulation among organisms is lacking in asexuals. Asexuals do form lineages and historical entities (individuals), but these are ontologically like clear-cut non-reticulating supraspecific monophyla and not like sexual species: "cladistic structure will go down to the organism level" (Mishler and Theriot 2000a, p. 51). This might warrant a dichotomous species pluralism (sexuals vs asexuals) so that what is called species in sexuals and asexuals is actually two biologically different kinds of entities. In line with this, many researchers do not accept asexual species or at least emphasize that they are not directly comparable, among them Mayr (1987, 2000a), Ghiselin (1997), Meier and Willmann (2000a), Bock (2004) and Dobzhansky: "the species as a category which is more fixed, and therefore less arbitrary than the rest, is lacking in asexual and obligatorily self-fertilizing organisms [. . .] The binominal system of nomenclature, which is applied universally to all living beings, has forced systematists to describe 'species' in the sexual as well as in the asexual organisms. [. . .] Nevertheless, systematists themselves have come to the conclusion that sexual species and 'asexual species' must be distinguished [. . .] In the opinion of the writer, all that is saved by this method is the word 'species.' A realization of the fundamental difference between the two kinds of 'species' can make the species concept methodologically more valuable than it has been" (Dobzhansky 1937, p. 321). Dobzhansky again points out here that our taxonomic nomenclature leads to the same kind of name (binomials) being assigned to what may be very different entities, which is a reminder that T species are not the same as E species. The arguments of those who hold that sexual and asexual species are not the same should not easily be dismissed as they imply that there is yet another form of homonymy of the term species involved. Certain species concepts such as the Evolutionary, the General Lineage or the Unified Species Concept explicitly embrace asexuals, and their adherents consider the fact that these concepts are flexible enough to cover the whole spectrum of reproduction an advantage. However, it could be argued that while different kinds of lineages (such as reproductively isolated lineages, those with different ecological niches, etc.) are rightfully subsumed under the same name ("species"), to include also asexuals may be stretching the lineage pluralism a bit too far.

What, then, could be arguments in favour of combining sexual and asexual organisms into the same kind of taxonomic unit ("species")? First of all, sexual and asexual reproduction are the extreme points in a continuum, with all sorts of intermediate (mixed) reproductive strategies in between (Mishler and Theriot 2000a). This in itself, however, is not conclusive evidence because, as is repeatedly argued in this book, fuzziness does not mean that boundaries do not exist. The groups that first come to mind when thinking about asexual reproduction are prokaryotes, but the main problem with these organisms may be a very different one, namely, that there is so much horizontal gene flow among them that it is doubtful that taxonomic individuation can be carried out in a way comparable to

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p. 297), but this seems not to have been the case as it was denied by Mayr later (see Stamos 2003, p. 150; Mayr 1987).

eukaryotes, and then a large part of asexuals will be something else than what we usually call species anyway (see Sect. 5.7). For eukaryotic asexuals, perhaps, the main argument in favour of their forming usual species is to do with cohesion. Genetic exchange via reproduction is viewed as one of the main forces of cohesion in sexual species. Beneficial mutations can spread through a population in selective sweeps, and the homogenizing effects of gene flow can keep populations or demes from diverging through drift. Asexuals have none of that. Still, they often form well-defined clusters in character space that are isolated from other such clusters: "One particular troublesome aspect of excluding nonsexual species is that most parthenogenetic 'species' display the same patterns of phenotypic cohesion within and discontinuity between as do sexual species" (Templeton 1989, p. 8). This has led some authors to doubt that gene flow plays a major role in cohesion (the locus classicus is Ehrlich and Raven 1969, but see also Grant 1980 and Lande 1980). As a consequence, Templeton's (1989) Cohesion Species Concept combines organisms into one species that shows phenotypic cohesion and genetic *and/or* demographic exchangeability: "For asexual taxa, genetic exchangeability has no relevance, and species status is determined exclusively by demographic exchangeability" (Templeton 1989, p. 21). A very similar view was already expressed by R. A. Fisher. Although he, too, makes a distinction between sexual and asexual species, he also regards exchangeability as a key criterion: "Species, properly speaking, we could scarcely expect to find [in asexuals], for each individual genotype would have an equal right to be regarded as specifically distinct, and no natural groups would exist bound together like species by a constant interchange of their germ-plasm. The groups most nearly corresponding to species would be those adapted to fill so similar a place in nature that any one individual could replace another, or more explicitly that an evolutionary improvement in any one individual threatens the existence of the descendants of all the others" (Fisher 1930, p. 121).

Many biologists will not be convinced that this suffices to combine sexuals and asexuals into the same notion of species. After all, even if gene flow through sexual reproduction does not play an important role in cohesion as often assumed, it still occurs in sexuals, and it does not in asexuals. This is still a fundamental difference between the two, or is it? In practice, this difference often simply does not exist. Think of allopatric sexual populations—they might exchange genes through reproduction, but they don't; they are as tokogenetically separate as asexual organisms. In the absence of gene flow, however, what else keeps the various separate populations of a sexual species together if not common selection pressures and a common history, i.e. a relatively recent common ancestor which may result in common developmental constraints, etc.? In other words, the very same processes are responsible for cohesion and thus for the phenotypic clustering and gaps that we find in asexual organisms! Therefore, unless we strictly classify allopatric populations of sexual organisms as distinct species, the distinction between sexuals and asexuals is not as clear-cut as often claimed. It is in this context that Templeton (1989, p. 9f.) writes "At what point is isolation by distance and population subdivision sufficiently weak to bring a taxa [sic] into the logical domain of the isolation and recognition concepts [i.e. sexual species concepts]? [...] there is a continuum from panmictic evolutionary dynamics to genetically closed evolutionary dynamics".

In a nutshell, there are differences between sexual and asexual species taxa, but just how pronounced they are is not at all clear (and may well vary from case to case). Whether sexual and asexual taxa can and should be subsumed under the same notion of E species (and not just T species in nomenclature) seems to be an open question. The important dimension of this conundrum is, ultimately, in how far biological analyses based on species taxa (their number, distribution, etc.) will be skewed by lumping sexual and asexual species. We may never definitively know, but this is only part of a larger problem that will be discussed in Chap. 7.

5.2 The Hierarchy of Species Concepts: The Evolutionary, General Lineage and Unified Species Concepts

> *I therefore believe myself to have found, on all essential points, the final solution of the problems. And if I am not mistaken in this belief, then the second thing in which the value of this work consists is that it shows how little is achieved when these problems are solved.*
>
> Ludwig Wittgenstein (1922), *Tractatus Logico-Philosophicus* (Preface, Pears/McGuiness translation)

A basic dilemma of the species problem as perceived by many has been formulated by David Hull. He lists three criteria that concepts in science are expected to fulfil: universality or generality, applicability and theoretical significance. The problem with available species concepts is, according to Hull, that none of them meet all three: "Most importantly, if a species concept is theoretically significant, it is hard to apply, and if it is easily applicable, too often it is theoretically trivial" (Hull 1997, p. 358). Add to this the problem of universality[4] (Hull explicitly mentions as intractable problems for species definition those of asexual reproduction and hybridization), and the prospects for a solution to the species problem are bleak. By separating theoretical significance from practical applicability and making a virtue out of their incompatibility, as it were, something like a solution has been found—although this solution admittedly only pertains to the theoretical dimension of the problem. The introduction of the notion of a hierarchy of species concepts in which a single one functions as a true ontological or primary concept and all the others as secondary species identification criteria has arguably been one of the major conceptual breakthroughs in recent decades.[5] The primary

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[4] According to Hull, universality of species concepts does not covary with either their theoretical significance or their applicability (Hull 1999, p. 42).

[5] Richards (2010, p. 143) states that if there are indeed two kinds of species concepts—an ontological one and several secondary criteria—then a framework like that of Hull where the perfect species concept should fulfil all three of his criteria "guarantees a species problem. We have treated […] concepts as competitors, rather than as complements". Hull (1999, pp. 38–43) briefly comments on why he (I think) seems to agree with Mayden's approach but justifies his own from a more open-minded philosophical and less involved (scientific) perspective.

concept (a term from Mayden 1997[6]) is that of species as lineages, either as defined by the Evolutionary Species Concept (see Mayden 1997, 1999, 2002; Wiley and Mayden 2000a, b, c) or the General Lineage or Unified Species Concepts (de Queiroz 1998, 1999, 2005a, b, 2007).[7] Importantly, it also embraces the view that *all* species concepts listed in Chap. 4 are based on biological realities, and that means that they may not be applicable to all taxa or situations but that they cannot be simply wrong.

Let us start with the Evolutionary Species Concept according to which species are ancestor-descendant lineages that evolve separately from other such lineages and have their own evolutionary tendencies and historical fate. This definition is something like the consensus definition of several publications (Simpson 1951, 1961; Wiley 1978; Wiley and Mayden 2000a), and it was probably not a coincidence that it was the palaeontologist (Simpson) among the main architects of the Modern Synthesis who came up with a notion of species as lineages through time. The second half of the concept ("own evolutionary tendencies and historical fate") is important in that it precludes the assignment of species status to each and every ephemeral offshoot of a species (e.g. small captive populations or a temporary, allo- or peripatric population) and therefore holds that there should be some kind of assessment of biological relevance involved when delimiting species in practice (see Chap. 6), which means that species delimitation is only possible in a meaningful way in hindsight. The Evolutionary Species Concept "demands only that speciation and evolution are natural processes involving lineages that maintain cohesion and have unique identities"—something that probably all biologists would agree is true—and thus has "the greatest generality" of all species concepts (Mayden 1997, p. 416). It is conceded that it is not operational, i.e. it will not help in a concrete case of whether a certain group of organisms form a species or not but "[w]hile this may be viewed as a possible shortcoming, it is not so for a primary concept" (p. 419) because it is about what a species is and not how to identify one. Therefore, "it requires bridging concepts permitting us to recognize entities compatible with its intentions. To implement fully the ESC we must supplement it with more operational, accessory notions of biological diversity—secondary concepts" (p. 419). The Evolutionary Species Concept is considered the single appropriate primary (ontological) concept because it unites all those entities that are identified as species by the other (secondary) species concepts which function as identification criteria. Mayden (1997, p. 414, 421) draws an analogy between the hierarchy of species concepts and phylogenetics: monophyly is defined as the property of a group of taxa to comprise all and only the descendants of a stem species (and that

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[6] Mayden (1997, p. 418) adapted it from Mayr (1957). See also Hey (2006, p. 448, Box 1 where Hey shows that Mayr did not follow up on this distinction) and de Queiroz (2005c) on Mayr's early role in the general conception of species as population or metapopulation lineages.

[7] Naomi (2011) summarizes both Mayden's and de Queiroz‘s approach and concludes that they are basically equivalent. Naomi presents what he calls a revised version of this integrated framework of species concepts, but I have to admit that to me he simply reformulates what Mayden and de Queiroz have stated.

very stem species), but this concept is not observable. Rather, a secondary concept, the existence of synapomorphies, functions as an operational way to identify monophyletic groups: "The concept of monophyly, like the ESC, is applicable but is in no way operational. Secondary concepts for both species and supraspecific categories are requisite in our discovery of species and supraspecific groupings, respectively" (p. 421). Richards (2010), who calls this hierarchical approach to species concepts the "division of conceptual labour solution", emphasizes that it is "theoretically monistic and operationally pluralistic" (p. 142), and Hey (2006, p. 447) even goes so far as to claim that "[m]uch of the debate in recent decades over [species] concepts, and over pluralism versus monism, can be seen as an unnecessary consequence of treating species identification criteria as if they were more fundamental concepts". And he ends his essay with a warning (p. 449): "As scientists we should not confuse our criteria for detecting species with our theoretical understanding of the way species exist [...] Detection protocols are not concepts. This point would be child's play if we were talking about electrons or disease agents, but because real species are so difficult to study, and because our best understanding of them includes their often being truly indistinct, we have had trouble separating the detection criteria from our more basic ideas on the existence of species".

One of the problems with species as lineages is that lineages exist on all levels within the Tree of Life: from cell lineages within organisms and gene trees through familial ancestral-descendant lines, populations and species to supraspecific monophyletic groups of increasing inclusiveness and finally the Tree of Life as a whole. Which level of lineages, then, is the species level? Wiley and Mayden (2000a), drawing on Hennig (1966), identify that level as the species level where tokogenetic relationships (horizontal reticulation through reproduction) dissolve into strictly hierarchical phylogenetic relationships. Therefore, "[a]ll evolutionary species are comparable because they are the largest tokogenetic biological systems" (Wiley and Mayden 2000a, p. 77). This seems a reasonable choice and may well be the best one, too. However, it is not unproblematic, particularly with respect to allopatric populations of sexual organisms and asexual organisms in general. But this is more to do with species delimitation and will be taken up again in Sect. 6.2.

Viewing species as lineages is an intuitive notion because dogs produce dogs, sheep produce sheep and humans produce humans; this is the core of what Wilkins has called the generative notion of species (see Chap. 2). It is also religiously intuitive because on the lineage view organisms of a species could be traced back to their first creation in a kind of "biblical coalescence". Importantly, it is also compatible with the ontological status of species as historical, spatiotemporally restricted individuals. It is therefore more general than relational species concepts: the Biological Species Concept, at least in most interpretations, regards species as reproductive communities isolated from *other* such communities, and the Hennigian Species Concept holds that species status is only meaningful *with respect to* a sister species. However, as Wiley and Mayden (2000b, p. 154) make clear: "the ontological status of species as individuals precludes relational species concepts. An entity either exists or it does not. Its existence does not depend on the presence or absence of another entity to provide its reality". My sister is my sister only because of my existence, but that does not mean that she only exists because of me: as an individual her existence is completely independent of mine. Consider also the very first species of life on earth. On a relational species concept, this group of organisms was not a species because nothing existed in relation to which it could have been a species.[8]

A very similar hierarchical approach was suggested by Kevin de Queiroz (1998, 1999, 2005b, 2007). His General Lineage and Unified Species Concepts, which are practically identical, are based on the insight that "almost all modern biologists have the same general concept of species" (de Queiroz 1998, p. 57). This common ground is again a lineage view of species: "All modern species definitions either explicitly or implicitly equate species with segments of population level lineages" (p. 60).[9] The way de Queiroz uses the term lineage is a little different from the usual way. It is already clear that he aims at the population level (not lineages of supraspecific monophyla), and this level is, according to de Queiroz, a continuum from the deme to the species. At this level, "a lineage is a population extended through time, and conversely, a population is a short segment, a more or less instantaneous[[10]] cross section of a lineage" (p. 60). Species as populations and species as lineages are therefore only time-limited (synchronic = horizontal) and time-extended (diachronic = vertical) versions of the same species concept (de Queiroz 1999, p. 54; contra Bock 2004 and others, see Sect. 1.4). A lineage at the level of populations or species is "a single line of descent. It can be represented on a phylogenetic tree as a set of branches that forms a pathway from the root of the tree (or some internal point) to a terminal tip" (de Queiroz 1998, p. 60). Lineages are always unbranched, and they need not be monophyletic (in fact, they often are not) and therefore must not be mistaken for clades! Figure 5.1 shows an illustration of this lineage concept.

Importantly, "[s]pecies do not correspond with entire population level lineages. If they did, species would be partially overlapping and *Homo sapiens* would be part of the same species as the common ancestor of all living things" (de Queiroz 1998, p. 60). Rather, species are "*segments* of population level evolutionary lineages" (ibidem, my italics), and these segments must be evolving separately from other such segments (species) (de Queiroz 2005b, 2007). This is an obvious parallel to the

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[8] Ernst Mayr (1970, p. 14) explicitly compares the concept species to that of brother and says: "The word 'species' likewise designates such a relational property. A population is a species with respect to all other populations with which it exhibits the relationship of reproductive isolation—noninterbreeding. If only a single population existed in the entire world, it would be meaningless to call it a species". See Sect. 5.3 for more on this.

[9] de Queiroz (2011) traces this lineage view back to Darwin who equated species with "branches in the lines of descent" (see also the only figure, the famous branching diagram, in Darwin 1859).

[10] *More or less* instantaneous because even the snapshot view of a synchronic population is not really atemporal since the processes that make up a population, such as interbreeding, are temporal phenomena, i.e. they occur in time.

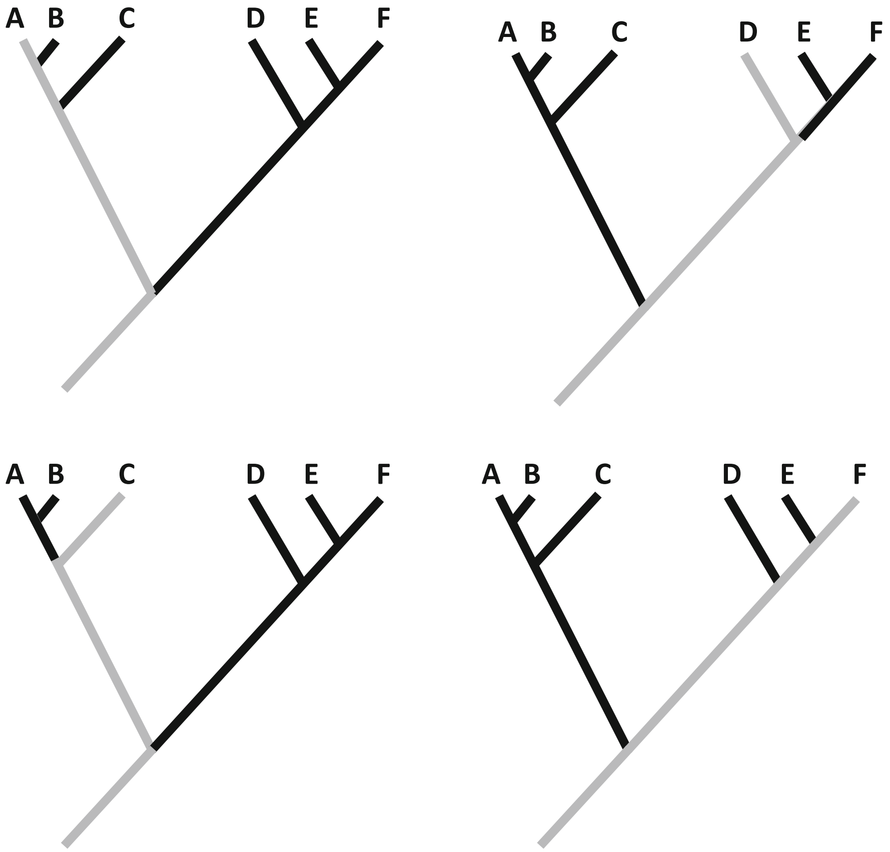

Fig. 5.1 Lineage concept sensu de Queiroz (1998, 1999). Lineages (*highlighted in grey*) are unbranched single lines of descent. They need not be monophyletic as they can pass through branch points. Note that not all lineages are shown

Evolutionary Species Concept where lineages must also evolve separately and have their own evolutionary tendencies and historical fate. And in line with the hierarchical approach of Mayden (1997), de Queiroz also regards the usual species concepts as species criteria that do not tell us what species are but that are operational in species identification and delimitation (Fig. 5.2).

Since speciation as the irreversible divergence of two population-level lineages is a time-extended process, the exact point in time where speciation is complete (the threshold beyond which lineage fusion is no longer possible) is hard or impossible to identify precisely. “The diversity of alternative species definitions—or more specifically, the diversity of alternative species criteria—is directly related to the diversity of events of subprocesses that occur during the process of speciation. Each criterion corresponds with one of the events that occurs during that process”

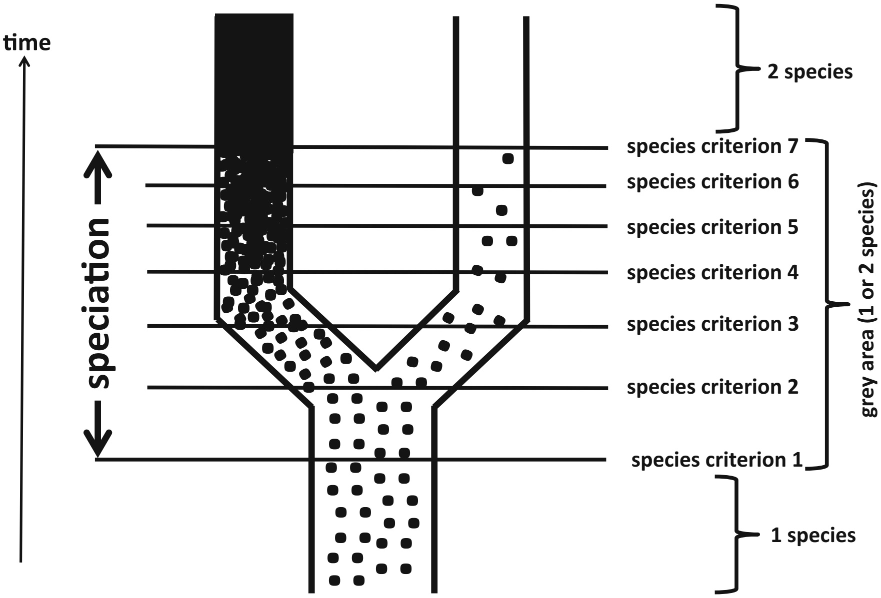

Fig. 5.2 Species lineages, species criteria and speciation. Speciation is the irreversible sundering of two population lineages. It is a process through time, and where along the time axis species status of the two new lineages is reached is ultimately a matter of convention. Different species concepts (here interpreted as species criteria; the number seven is arbitrary) will make different biological phenomena the basis for deciding if speciation is complete or not, for example, reproductive or genetic isolation, different ecological niches, diagnosability, reciprocal monophyly and so forth. However, all agree on species being independent population lineages. Modified after Fig. 5.4 in de Queiroz (1998) and Fig. 3 in de Queiroz (2005b). Below and above the grey area there will be agreement on the number of species (one and two, respectively), but within the grey area different species criteria come into conflict as to the number of species

(de Queiroz 1998, p. 64). This is why, as stated above, all species concepts or criteria refer to biological realities and cannot simply be wrong. However, the secondary concepts or criteria now no longer function in species conceptualization but are instead relevant for species delimitation (de Queiroz 2007). This will lead to conflicts (the grey area in Fig. 5.2), but since each one of them is evidence for the existence of a species, the more of these criteria are met, the higher the degree of corroboration of the species hypothesis (de Queiroz 2007).

This is more or less in line with Mayden's (1997) hierarchy of species concepts, and Mayden (2013) holds that the General Lineage Species Concept and the Evolutionary Species Concept are synonymous (see also Naomi 2011). However, de Queiroz goes one step further. To him, all lineages are ultimately species, at least for the time being. He compares the process of speciation with that of growing up, and there are different criteria by which an adult can be identified (e.g. certain secondary sexual characteristics or functional gametes). So far, so traditional, but "If the species category is to have the general theoretical significance that we so often claim for it, then it probably should not be treated as analogous to the category *adult*; instead, it should be treated as analogous to the category *organism* [...] If the concept of the species is to have comparable theoretical importance, it must refer not to a stage in the separation and divergence of lineages but to entire lineage segments, from initial separation to extinction. An important consequence of this minor yet fundamental conceptual and terminological shift is that the various criteria discussed above would no longer be species criteria—at least not in the sense of standards for granting lineages taxonomic status *as species*. Instead, they would be criteria for different stages in the existence of species—the diagnosable stage, the monophyletic stage, the reproductively isolated stage, and so on" (de Queiroz 1998, p. 71). The competition between different concepts would thus vanish. However, and de Queiroz is well aware of this, species delimitation in practice would still be difficult and fuzzy, but the conceptual side of the species concept problem would be largely (dis)solved.

Expectedly, the hierarchical approach of Mayden and de Queiroz has not remained uncriticized. Richards (2010) fully embraces the hierarchy of species concepts as the "division of conceptual labour solution" to the species problem, and according to him, the Evolutionary Species Concept as the primary ontological concept does justice to both the synchronic and the diachronic dimension of species: "This theoretical species concept satisfies the historical component implicit in evolutionary theory by virtue of being a historical lineage connected by ancestor-descendant relations. And given that this is a lineage of *populations*, it also satisfies the synchronic component of species as groups of organisms at particular times" (Richards 2010, p. 132). Other philosophers, however, are critical. Ereshefsky holds that a general lineage approach only masks the heterogeneity of the species category because "what constitutes a lineage has multiple answers, and those answers vary according to which species concept one adopts" (Ereshefsky 2010a; Ereshefsky is a lineage pluralist, see Sect. 3.6), but I do not think that there is much disagreement among biologists in this regard. Pigliucci (who is both a biologist and a philosopher) thinks the concept of lineage too broad to be useful because it only picks out a necessary condition (population-level lineages) that is, however, "not sufficient for being a species" (Pigliucci 2003, p. 598). de Queiroz rebuts this criticism by saying that it is both a necessary and sufficient condition for being a species and not only that but that this is the only such condition: "An important corollary of the metapopulation lineage proposal is that all separately evolving metapopulation lineages are species" (de Queiroz 2005a, p. 1265). He thinks that the metapopulation lineage solution and Pigliucci's family resemblance approach are compatible because they solve different species problems or aspects thereof: "These two proposals are highly compatible. According to the metapopulation lineage proposal, the species category is best defined with reference to a single necessary and sufficient property—existence as a separately evolving metapopulation lineage. Nonetheless, in agreement with the cluster concept proposal, the idea of a metapopulation lineage may itself be best interpreted as a family resemblance or cluster concept" (p. 1267). Of course, the devil is in when exactly two lineages should be considered to be "separately evolving", again highlighting that the hardest part of the species problem is delimitation, not definition.

Stamos (2003, p. 279ff., 322f.) is also much less impressed than Richards (2010) by the idea that all species concepts conceive of species as lineages and that the species problem can theoretically be solved by accepting the lineage ontology as the primary species concept and by viewing the majority of species concepts as secondary species identification criteria. In fact, Stamos denies that all species concepts are based on the idea of a lineage. He explicitly names the morphological and the cluster concepts (phenetic and genotypic cluster). While it is true that these concepts do not *explicitly* contain the idea of a lineage, I still think that Stamos is wrong here, for a very simple reason: what else should species be if not lineages? They are historical entities, and as such (given our present understanding of evolution), whatever else they may be, they must be lineages as well. I doubt that the proponents of the morphological and cluster concepts would deny that, and de Queiroz (1998, p. 63, my italics) explicitly says that "[e]ven the seemingly most radical modern species definitions [one of the concepts he mentions is the Phenetic Species Concept] are *at least consistent with* the general lineage concept of species". In any case, while Mayden's hierarchy of species concepts and the similar approach of de Queiroz's General Lineage/Unified Species Concept have met with approval by both biologists and philosophers, Stamos is rather dismissive of Mayden's approach which he only grants a few lines in his book (he does discuss the General Lineage Concept in more detail, though). He only calls it a "simplistic solution" (Stamos 2003, p. 322) and claims that the "hierarchy quickly falls" (p. 323) because it "fails to address the many problems with Simpson's species concept" (i.e. the Evolutionary Species Concept) and also to "acknowledge that most of the species concepts which Mayden classifies as secondary are not congruent in their division of organisms into species" (p. 323). I do not see why this latter point is crucial, though. It is well known that hardly any two species concepts are fully congruent. That is one of the core issues of the species problem. What Mayden's and de Queiroz's hierarchy does, however, is show that this discordance may not be on the ontological but rather on the operational level. I am sure that Stamos would disagree with this statement, but perhaps what he mainly objects to is the optimism that he considers premature ("problem solved", see the term "denouement" in the title of Mayden's paper). My own interpretation of this "denouement" has always been that the problem has been laid out more clearly by no longer conflating different types of species concepts (true concepts and identification criteria), not that it has been properly solved (quite to the contrary, hence the Wittgenstein quote as the motto of this section). On this view, the problem has shifted from ontology to operationality, i.e. from species definition to species delimitation. However, being a biologist, I may be biased towards the practical relevance of delimitation because ultimately, this is what much of biology is either directly dealing with (taxonomy) or dependent upon in various applications in evolutionary biology, ecology and other disciplines. I will certainly not tell philosophers when they should consider one of their problems solved, but perhaps it is fair to say that from the *biological* perspective, the theoretical question of what a species is has been given an acceptable answer (or at least as acceptable an answer as is obtainable), and that the main *biological* problem remaining is to do with delimitation and its corollaries rather than conceptualization.

5.3 The Biological Species Concept

Probably, more has been written about the Biological Species Concept than about any other, and it is the most widespread species concept among nonexperts, dominating undergraduate and school textbooks. This is very likely due to two reasons: it is intuitive and it was promoted most successfully. The concept is intuitive in two ways: (1) reproduction is a very obvious property of living organisms, and dogs mate with dogs, humans with humans and so on, and (2) the highest level of interfertility often coincides with our intuitive classification of organisms based on their similarity ("folk taxonomy"). By the most successful promotion, I refer to the fact that the Biological Species Concept is the main concept of the Modern Synthesis and was therefore supported by some of the most influential evolutionary biologists of the twentieth century, most notably of course by Ernst Mayr. Although he was not the first to adhere to it, Mayr is the one who popularized this species concept, and he has repeatedly discussed and explicated it (e.g. Mayr 1940, 1942, 1963, 1982, 2000a, b, c[11]). However, it or something very similar can be found in many earlier and contemporary biologists (e.g. Poulton 1904; Jordan 1905; Dobzhansky 1935, 1937). Since interbreeding is so obvious a quality of organisms, it has been a criterion for species delimitation and definition for a long time, for example, in Buffon and even Frederick II of Hohenstaufen. In fact, "[l]ack of interbreeding has played a role in many, if not most, conceptions of natural or biological species since the Greeks" (Wilkins 2009b, p. 136; see also Sect. 2.2). Mallet gives a summary of the origins of the Biological Species Concept at the beginning of the twentieth century (Mallet 2004a), and then, starting with Dobzhansky's 1935 paper, also takes ideas about group selection into account (Mallet 2010). It has already been stated that the names of species concepts are historically contingent, and the fact that this concept is called biological does not mean that others are not. Mayr (1970, p. 12f.) explains that the name *Biological* Species Concept was chosen "not because it deals with biological taxa, but because the definition is biological. It utilizes criteria that are meaningless as far as the

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[11] Mayr (2000a, b, c) are Mayr's three contributions to the volume on *Species Concepts and Phylogenetic Theory* (Wheeler and Meier 2000). Mishler and Theriot (2000c, p. 181), in the same volume, say about Mayr's chapters (particularly Mayr 2000b): "There is little we can reply to Mayr that has not been said before by us and others. His arguments are based on authority alone. He mainly resorts to empty name calling and dogmatism; he simplistically labels his opponents as typologists, nonbiologists, and so forth. We particularly resent his characterization of us (presumably) as 'armchair taxonomists'". Although the general tone of the contributions in this volume is objective, Mishler and Theriot are, unfortunately, right about Mayr here.

inanimate world is concerned". The word "biological" originally does not distinguish this concept from other concepts of living species but from the use of the term species in the context of nonliving things (which was very common at least until the eighteenth century). There are many different definitions of the Biological Species Concept, and I will not discuss all of them in their subtle differences but rather highlight a number of interesting and important issues to do with this notion of species. Most, if not all, readers will be familiar with this species concept anyway.

A classical definition of the Biological Species Concept is this one: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942, p. 120). There are several other formulations by Mayr, including one emphasizing ecological niches (see footnote 3 in Sect. 5.1). Two parts of this definition need further explication. Reproductive isolation does not mean that reproduction is impossible. Bock (2004) emphasizes that horses and donkeys, which can successfully mate but whose offspring are (usually) sterile, are obviously not reproductively isolated but that they are genetically isolated, which is why he replaced "reproductively" with "genetically" in the definition. What is meant, in other words, is the lack of gene flow that defines the boundaries between species. This use of genetic isolation, however, is different from the one in the Genetic Species Concept where genetic isolation is not the same as lack of gene flow (Sect. 5.4). The second important part of the definition is "actually or *potentially* interbreeding populations". The "potentially" is part of the definition in order to allow for allopatric populations to be part of the same species because by definition allopatric populations cannot interbreed. Interbreeding therefore becomes interfertility which denotes a possibility rather than an actuality: "For species to be reproductively isolated is the same thing as not to have the potentiality to interbreed" (Ghiselin 1997, p. 96), i.e. reproductive isolation is due to intrinsic isolation mechanisms, not due to extrinsic factors such as a geographical barrier. However, "[w]hat matters is not that all gene flow be cut off, but that it be cut off to a sufficient degree that the species can continue to diverge instead of fusing back together into a single populational individual" (ibidem). Therefore, Ghiselin offers an alternative formulation: "Biological species are populations within which there is, but between which there is not, sufficient cohesive capacity to preclude indefinite divergence", of which he also gives "a more colloquial, jocular equivalent: Biological species are the most incorporative [= inclusive, see Sect. 3.1] reproductive populations with enough 'sticktogetherness' to make them hang in there as evolutionary units" (Ghiselin 1997, p. 99). This is closer to the Genetic Species Concept and in line with Mayr's interpretation of biological species whose basic characteristic is the "protection of harmonious gene pools" (e.g. Mayr 1970, p. 13; Mayr 2000a, p. 23).[12]

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[12] The emphasis on protected gene pools seems to be a later development in Mayr's notion of species (see Wilkins 2009a, p. 191f.). Rather than just giving a descriptive definition (reproductive isolation), Mayr now emphasizes the adaptive side of being a species: "A species is a protected gene pool. It is a Mendelian population that has its own devices (called isolating mechanisms) to

Because sexual reproduction lies at the very heart of this concept, the Biological Species Concept is not applicable to asexual organisms, which has repeatedly been emphasized (e.g. Ghiselin 1987b; Mayr 1987, 2000a; Meier and Willmann 2000a). However, the Biological Species Concept is most widespread among taxonomists who deal with groups where asexual reproduction does not occur, like mammals and birds (Mayr was originally an ornithologist[13]), and this is probably why E. O. Wilson said that it "works well enough in enough studies on most kinds of organisms, most of the time" (Wilson 1992, p. 45). This, however, may be too optimistic, and even if it were true, there are other problems with its applicability that confirm Mayden's (1997) conclusion that the Biological Species Concept cannot function as a primary ontological species concept. First of all, but that applies to all species concepts, species boundaries in nature are inherently vague and that also holds for reproductive or genetic isolation, which is a matter of degree (Ghiselin 1997, p. 100).[14] Interbreeding is a continuum, from complete panmixia to a complete lack of interbreeding, but between closely related forms, these extremes may be the exception rather than the rule. Not every single mule is sterile; big cats produce fertile hybrids in captivity (mostly females, in line with Haldane's rule), and there are genera that are notorious for their otherwise "good" but hybridizing species, e.g. the deer genus *Cervus* (McDevitt et al. 2009), the hare genus *Lepus* (Alves et al. 2008) and the dog genus *Canis*. In the latter, a recent study has found hybridization with fertile hybrids between golden jackals (*Canis aureus*) and domestic dogs (which are, zoologically, wolves) including backcrossing (Galov et al. 2015), and the North American red wolf (*Canis rufus*) is often believed to be the product of hybrid speciation with grey wolves (*Canis lupus*) and coyotes (*Canis latrans*) as parental species.[15] An even more revealing example comes from ornithology: no less than 418 different interspecific hybrids have been found among 126 out of 149 species of ducks (Anatidae), with 20 % of the hybrids found to be fertile (Scherer and Hilsberg 1982; see also McCarthy 2006). This is the background against which Coyne and Orr (2004, p. 30) summarize their view like this: "distinct species are characterized by *substantial but not necessarily complete reproductive isolation*. We thus depart from the 'hard line' BSC by

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protect it from harmful gene flow from other gene pools" (Mayr 1970, p. 13). With this formulation Mayr shows how similar his notion is to the Genetic Species Concept (see Sect. 5.4).

[13] While it is probably true that the Biological Species Concept is the most popular among mammalogists and ornithologists, this does not mean that it is the only or even dominant species concept in these disciplines, particularly when the actual practice of species description and delimitation in taxonomic studies is concerned. Sangster (2014) argues that avian species-level taxonomy has been pluralistic since the 1950s and that two criteria of Phylogenetic Species Concepts, diagnosability and monophyly, have often been used as the arbiter for species status.

[14] The Hennigian Species Concept only accepts species in the case of *absolute* reproductive isolation, which, however, leads to other serious problems (see Sect. 5.5).

[15] It has, in fact, been tried to make the category of the genus more objective by defining it as containing all species that are able to produce adult F_1 hybrids, regardless of their being fertile or not (Dubois 1988, cited from Minelli 2000, p. 344f).

recognizing species that have limited gene exchange with sympatric relatives. But we feel that it is less important to worry about species status than to recognize that the *process* of speciation involves acquiring reproductive barriers, and that this process yields intermediate stages when species status is more or less irresolvable".

The Biological Species Concept faces two other serious problems that limit its applicability: space and time.[16] Species exist in different places and through time, but the Biological Species Concept is only directly applicable if the organisms under study live in sympatry in the same time horizon. Mayr was well aware of this: in later definitions the word "potentially" is often missing (e.g. Mayr 1970, p. 14), and species are only thought of in a completely non-dimensional way: "The biological species concept has its primary significance with respect to sympatric and synchronic populations (existing at a single location and at the same time), and these, the 'nondimensional' species—are precisely the ones where the application of the concept faces the fewest difficulties. The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other, but also the more irrelevant biologically this becomes" (Mayr 1970, p. 13; see also Mayr 2000a, p. 27; and Bock 2004 who even confines the term species to the synchronic dimension and uses "phyletic lineage" for the diachronic dimension). Mayr admits that the species status of allopatric and allochronic populations can only be determined based on inference or subjective criteria but (correctly) adds that this is by no means a peculiarity of the Biological Species Concept (Mayr 2000c, p. 162) and summarizes: "species taxa are multidimensional, but the nondimensional situation is required to determine the crucial biological properties of the species concept" (ibidem, p. 166). Adherents of the hierarchical approach to species concepts outlined in Sect. 5.2 would of course agree that this is true for the Biological Species Concept—which is exactly why this concept is a secondary identification criterion and not a primary (ontological) concept.

The Biological Species Concept, according to Mayr, is not only non-dimensional but also relational: species only exist in relation to other reproductively isolated species. This has already been mentioned in Sect. 5.2, and it has been emphasized that, while species of course have relations with each other (isolation, various degrees of phylogenetic relatedness, etc.), regarding them as existing *only* (or even just primarily) in relation to other species is a serious contradiction to their being historical individuals (see also Stamos 2003, p. 197 on this). Consequently, Ghiselin (1974a, 1997, p. 110) argues that the Biological Species Concept is not inherently relational and that species are simply "reproductively isolated from any other such groups *as may happen to exist*" (my italics). That the species status of spatially or temporally distant populations becomes biologically less relevant, as Mayr claims, is also doubtful, if not outright wrong. It may be true for the study of speciation itself, i.e. the divergence of population-level lineages, but species status

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[16] "The temporal dimension is not the friend of the biological species concept", as Cracraft (1987, p. 340) put it.

is important for many different kinds of biologically relevant analyses, among them comparative diversification rates among higher taxa and the distribution of biodiversity in space (macroecology) and time (palaeontology). Mayr seems to be making a virtue of necessity here by simply claiming that the areas where his favourite species concept faces difficulties are less relevant.

In any case, in taxonomic practice one rarely deals with such limited conditions as sympatry and synchrony combined. How, then, should one deal with allopatry, parapatry and allochrony under the Biological Species Concept? For parapatry, Corbet (1997), in an article advocating the Biological Species Concept in mammals, distinguishes three different scenarios: (1) diagnosable parapatric forms with minimal hybridization should be classified as distinct species (his example is from hedgehogs: *Erinaceus concolor* (now *E. roumanicus*) and *E. europaeus*); (2) diagnosable parapatric forms with substantial hybridization should be classified as subspecies (his example is house mice: *Mus musculus musculus* and *M. m. domesticus*); and (3) parapatric forms with minimal differences and some hybridization should also be classified as subspecies rather than species (the example being the mole rat *Nannospalax ehrenbergi* that comprises groups differing in karyotype). Of course, even with this guideline, there will be many borderline cases. However, the situation is not nearly as bad as with allopatric populations where interbreeding is lacking per definition. This lack can be due to extrinsic (spatial) separation only or due to intrinsic incompatibilities (genetic, physiological and/or behavioural and ecological). Organisms from allopatric populations could be brought together, for example in captivity, to see if reproduction occurs and if it results in viable and fertile offspring, but these conditions are highly artificial. And this option completely fails in the case of allochronic populations: while I have little doubt that in theory I could have viable and fertile children with, say, Cleopatra, there is no way of testing this. The usual way of settling the species status of such populations is by inference: instead of interbreeding other characters (mostly morphological in the case of fossils or subfossil, but also genetic, behavioural, etc.) are compared between the allopatric or allochronic populations, and if the similarity found is of the kind and degree usually found in "good" interbreeding sympatric species, then the two populations will be classified as conspecific; if not, they will be considered two distinct species (e.g. Mayr and Ashlock 1991, p. 104f.). This seems an obvious and intuitively sensible approach, but I do not think it is. First of all, reproductive isolation can in some cases be due to single "speciation genes" that do not affect the phenotype in any other substantial way (Nosil and Schluter 2011; for an example in *Drosophila*, see Phadnis and Orr 2009). Secondly, it could be argued that if species are to be regarded as independently evolving lineages, then it should not matter whether the independence is due to intrinsic or extrinsic factors (although, admittedly, intrinsic factors are more likely to result in permanent and irreversible separation). But the main error in the rationale behind this inferential way of classification is the implicit assumption that evolution proceeds in the same way in allopatry as it does in sympatry. This, however, is not the case. In sympatry there is selection against hybrids of reduced viability and/or fertility and fecundity, leading to the accelerated evolution of isolation mechanisms and reinforcement of differences in mating behaviour, reproductive anatomy, etc. In allopatry and allochrony, on the other hand, there is neither a need nor an opportunity for this kind of selection pressure. The two populations will diverge due to different selection regimes and genetic drift, but characters involved in the potential interbreeding will be largely governed by the latter: "Hybrid sterility or inviability might therefore be a simple byproduct of the divergence of genomes that are geographically isolated" (Coyne and Orr 2004, p. 269). Cracraft (1989, p. 37) agrees with this: "Reproductive isolation [. . .] is not an intrinsic attribute of populations; it is instead a relational concept. Populations do not evolve reproductive isolation. [. . .] Reproductive isolation is best interpreted as an epiphenomenon or effect of differentiation". As a consequence, even long-separated taxa can be interfertile upon secondary contact. Kunz (2012, p. 150) gives Old World and New World Ruddy ducks as an example. In this case, their interfertility is even a conservation issue because the translocated New World species (*Oxyura jamaicensis*) threatens the genetic integrity of its Old World relative (*Oxyura leucocephala*) in Europe. Mallet (2005, p. 229), in a review article, confirms that this is a rather common phenomenon: 25 % and 10 % of plant and animal species, respectively, are "involved in hybridization and potential introgression with other species. Species in nature are often incompletely isolated for millions of years after their formation". Of course it could be argued that then they have never been true species in the first place, but this is beside the point. The important fact is that lineages that evolve overall separately remain interfertile for a very long time in many cases.

Allopatric (and allochronic) populations are the most difficult to evaluate taxonomically, and a strict interpretation of species as gene flow communities entails that allopatric populations must be considered different species for as long as they are separated (Kunz 2012, p. 166; see also Sect. 6.1). This is for the sake of logical consistency because of the absence of any non-arbitrary demarcation criterion, but of course it is neither feasible nor desirable for biologists to implement this conclusion in taxonomic practice.

To conclude, the Biological Species Concept is the perfect yardstick of species status when and if it is applicable; unfortunately, that is very rarely the case and only applies to sexually reproducing organisms in the same place at the same time. And even then, strictly speaking, only the lack of hybrids is conclusive evidence (for two distinct species); occasional hybridization is more difficult to evaluate and ultimately needs some kind of arbitrary cut-off criterion. Mishler and Theriot (2000b, p. 123f.) have called the Biological Species Concept both "unapologetically nonuniversal" and "unapologetically nondimensional". Contrary to E. O. Wilson's quote above, most of the time, they are right.

5.4 The Genetic Species Concept

It has been repeatedly stated that reproductive isolation among otherwise "good" species is often not absolute. Van Valen (1976, p. 235) calls "broadly sympatric species that exchange genes in nature" multispecies, but the same phenomenon can be found with allopatric species. The insight that interbreeding and gene flow do not necessarily undermine the existence of two separately adapted integrated gene pools is at the heart of the Genetic Species Concept which Baker and Bradley (2006, p. 645) define like this: a species is "a group of genetically compatible interbreeding natural populations that is genetically isolated from other such groups". The accumulation of genetic changes in two diverging lineages during speciation creates "genetic isolation and protection of the integrity of the two respective gene pools" (ibidem). This is almost identical with Mayr's later explications of the Biological Species Concept, and the two are obviously very similar. The Genetic Species Concept takes this insight more seriously, though, as it considers populations as distinct species even if there is gene flow and fertile hybrids, while under the Biological Species Concept, such populations are usually classified as subspecies. There are a number of examples where, according to the Genetic Species Concept, there are two species, while adherents of the Biological Species Concept only accept one (or at least are undecided). Baker and Bradley (2006) give several mammalian examples such as the African savanna and forest elephants (*Loxodonta africana* and *L. cyclotis*)[17] and mule and white-tailed deer (*Odocoileus hemionus* and *O. virginianus*). Many more examples from basically all taxa could be listed here. Many of these genetic species pairs or groups will be morphologically very similar or even nearly identical (cryptic species), and for mammals Baker and Bradley (2006) give an estimate of more than 2000 unrecognized species. The emphasis on integrated or coadapted gene pools that would be disrupted and suffer a decrease in fitness through genetic incompatibilities in the wake of hybridization goes back to Bateson, Dobzhansky and Muller, although this idea is often just called the Dobzhansky–Muller model (Coyne and Orr 2004). It is also at the heart of the Differential Fitness Species Concept (Hausdorf 2011, see Chap. 4). While there are certainly incompatibilities among the genomes of different species, more recent research suggests that large parts may also be compatible (Mallet et al. 2016).

Operationally, as a means to detect species according to the Genetic Species Concept, Bradley and Baker (2001) suggest genetic distance values as a quantitative proxy for (potential!) species status. Based on cytochrome b sequence analyses in a number of bat and rodent species, they found that distance values below 2 % were typical of intraspecific variation, whereas values above 11 % were most often correlated with species status; anything in between could be either. The use of this genetic proxy is not why the species concept is called "genetic", and the authors are

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[17] For recent evidence as to the genetic distinctness of savanna and forest elephants, see Mondol et al. (2015).

well aware of this and make it very clear that these values are only indications where further research is most promising and that they do not imply a phenetic definition of the species category.[18] Of course, the Genetic Species Concept also faces the problem of allopatric distribution. Baker and Bradley (2006) suggest genetic distance values usually found in known sister species to function as the yardstick for the assignment of species status, but this is merely a convention that will often not correctly represent biological reality. In sympatry, the lack of sterile hybrids is conclusive evidence of two isolated gene pools and thus two species. The reverse, however, i.e. the existence of fertile hybrids, is more difficult to evaluate and will often require detailed genetic analyses and data on the fitness of the hybrids. In the case of geographically limited parapatric hybrid zones beyond which hybridization is insignificant, the two populations can be classified as different species under the Genetic Species Concept: "Unless the hybrid zone is of recent origin, a narrow geographically restricted hybrid zone is evidence of genetic isolation and consequently both phylogroups have a high probability of an *independent evolutionary fate*" (Baker and Bradley 2006, p. 654, italics added). The last three words of this quotation neatly show that the Genetic Species Concept can be interpreted as an application of the more fundamental Evolutionary Species Concept. The question when exactly two gene pools can be considered isolated once more reveals the problem that pinpointing exact boundaries is all but impossible where nature is inherently messy. This becomes particularly apparent when looking at how complex hybrid zones and gene flow can be. This has recently been shown in a genomic analysis of a classical textbook example: carrion and hooded crows (*Corvus corone/cornix*). These two corvids form a narrow hybridization zone throughout Europe, beginning in the north of the British Isles, running through Germany and Austria and then south of the Alps to the Mediterranean. They have variously been classified as conspecific (e.g. Haring et al. 2012) or as different species (e.g. Parkin et al. 2003; dos Anjos et al. 2009), and Poelstra et al. (2014) have now revealed that the phenotypic differences between the two taxa are due to differential gene expression in a small "speciation island" of less than 2 megabases which makes up less than 0.28 % of the total genome, while otherwise genetic introgression was common across the genome and, geographically, far beyond the narrow hybrid zone. In particular, the German carrion crows (just west of the hybrid zone) were overall genetically more or less hooded crows—except for their carrion crow-specific genotypes at the speciation island. This example shows that the notion of combined or separate gene pools sometimes is too coarse: obviously, there are intragenomic "sub-gene pools", some of which are permeable to gene flow, while others are not. How this can and should be translated into an

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[18] The values of interspecific divergence at the cytochrome b gene are different in other, and not consistent among, vertebrate groups (Johns and Avise 1998). See also Ferguson (2002) for a critical discussion of genetic divergence and species identification.

unambiguous, objective (but at the same time also biologically meaningful) taxonomic classification is anyone's guess.[19]

5.5 Cladistically Based Species Concepts and the Hennigian Convention

A number of species concepts make specific reference to the theory of cladistics. Although the phylogenetic species concepts certainly fall within this category, I am particularly referring to the Hennigian, cladistic and internodal species concepts in this section because it is these concepts that are based on the idea that species are delimited by speciation events and/or extinction, i.e. a species comes into being when a stem species splits into two daughter species, and it ceases to exist when it either becomes extinct or undergoes speciation itself. The former (extinction) is obviously undisputed, but the latter has triggered a seemingly endless discussion on whether stem species become extinct or dissolved, as it were, upon speciating or not. That there cannot be a surviving stem species goes back to Willi Hennig (1966) and has therefore been called the Hennigian Convention (elsewhere it is called deviation rule). Interestingly, Hennig's view on species was very similar to the Biological Species Concept (extended through time), and therefore Meier and Willmann (2000a, b) and Willmann and Meier (2000) call their species concept Hennigian Species Concept, which is indeed a combination of a very strict version of the Biological Species Concept and the cladistic species concept sensu Hennig or Ridley (1989). What sets it apart is that it requires *absolute* reproductive isolation, i.e. distinct species status for two populations is only granted if there are no fertile hybrids at all, not even one—which is why Wiley and Mayden (2000b, p. 146) call it the "hyperbiological species concept".[20] Since some female mules are fertile, horses and donkeys would have to be a single species. However, since domestic donkeys are closer phylogenetically to wild asses and zebras than to domestic (or wild) horses (Vilstrup et al. 2013), this also means that all extant *Equus* taxa would be numerically one and the same species. I doubt that many biologists would find this a desirable classification if the species category is to represent the lowest

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[19] It should be noted that it is situations like these that are underlying the notion of the Genic Species Concept (Wu 2001a, 2001b) that emphasizes adaptations whose genetic basis is distinct in two taxa, regardless of differentiation elsewhere in the genome. My guess would be that under this concept the two crow taxa would be granted species status. It has to be stressed, though, that, again, a cut-off criterion is needed to decide when exactly the conditions are met in such a way that species status is warranted. The Genic Species Concept, like any other species concept, is not immune to the continuousness of the evolutionary process and concomitant grey areas.

[20] Meier and Willmann (2000a, p. 38), citing earlier works of Willmann (1985, 1989, 1991), say that "the Hennigian Species Concept is identical to the Biological Species Concept if absolute isolation is adopted as the criterion for contemporaneous populations and the origin of the isolation of two sister species is used to delineate species boundaries in time".

distinct suprapopulational evolutionary unit. The rationale behind absolute reproductive isolation is that only absolute isolation is unambiguous; as soon as a certain level of hybridization is allowed, one has to agree on a threshold value, which is "entirely arbitrary" (Meier and Willmann 2000a, p. 40). They are aiming for logical consistency and do not allow for any element that might introduce vagueness into their concept (which is exactly why they also endorse the Hennigian Convention). However, while categories and definitions should always aim for precision, nature is inherently vague and messy, and by neglecting this important aspect of reality, they are throwing the "biological" baby out with the bathwater of logic. In other words, they are sacrificing biological relevance on the altar of logical consistency. Absolute reproductive isolation is certainly sufficient for species status, but is it also necessary? Do we really want to lump all lineages that for all intents and purposes evolve independently and have done so for a long time into a single species just because this is what we can do in a completely non-arbitrary fashion? What this boils down to in practice is that we just move up the taxonomic hierarchy until we are at a level where different lineages have been separated for so long that they have long left the grey area in Fig. 5.2. We would simply be avoiding the vagueness around the tokogeny/phylogeny divide by going up the hierarchical levels in the Tree of Life until populations are no longer so closely related to one another that tokogeny comes into play. In other words, we would be shifting the species level to what today is a supraspecific level to circumvent the problems that come with nature's fuzzy boundaries. But even if we did that, we would not rid ourselves completely from arbitrary decisions because the problem of allopatric populations would still be very real: they are separate, but should we assign them species status only because of their allopatry? Just like adherents of the Biological Species Concept, Meier and Willmann (2000b, p. 177) retreat to the flawed approach of using "the same morphological cues for species recognition that are also used in the sympatric situation". And thus, just like any other species concept, the Hennigian Species Concept is not able to remove threshold decisions completely. One could also argue that, while any concept allowing for occasional gene flow between distinct species must make a decision about a threshold, this decision is subjective, but not completely arbitrary. After all, there are criteria by which independence of gene pools and thus independence of lineages can be evaluated.[21] These criteria are themselves continuously variable, but this is not a shortcoming of taxonomy or biology but instead inherently natural and in this sense real. What is biologically relevant is that two lineages evolve separately, and occasional gene flow may not be a better argument for a single species than is the existence of German loanwords for the claim that English and German are the same language: "What matters is not that all gene flow be cut off, but that it be cut off to a sufficient degree that the species can continue to diverge instead of fusing back together into a single populational individual" (Ghiselin 1997, p. 96).

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[21] For example, reduced fitness in hybrids, equilibrium states of gene pools with respect to Hardy–Weinberg expectations, mutation, drift and selection, etc.

The aim for logical consistency also lies behind the Hennigian Convention, i.e. the notion that ancestral or stem species must go extinct (i.e. renamed as a new species) upon giving rise to daughter species. This is one of the most heated debates when it comes to temporal species delimitation because it produces counterintuitive taxonomic situations such as when in peripatric speciation a small isolated population attains species status: in this case the parental stem species would have to change its name even if it did not change at all.[22] What is even more bizarre and counterintuitive is that the (taxonomic) fate of the ancestral species solely depends on the fate of the peripatric isolate: if the latter dies while rafting to an island, the ancestral species stays the same species; if it makes it onto the island and eventually is considered a new species, then the ancestral species needs a new name and is regarded as a daughter species, just like the peripatric isolate. It is very clear, at least in this extreme scenario, that this is more a logical than a biological issue. Therefore this "Hennigian extinction" (Wilkinson 1990) has been seen as a formal issue rather than a biological one: "it seems to me that the critics have overlooked the most charitable interpretation of the Hennig Convention—it is a convention about *naming* and *denotation*. In short, the name of a species is extinguished at speciation. This follows from Hennig's views about the task of systematics. Using (and citing) Woodger and Gregg [. . .] and the views of Woodger (1937) in particular about sets in classification, Hennig strives to ensure that there is no ambiguity of reference in the sets named in systematics. Since as soon as a set is divided there is ambiguity, which of the two resultant sets is being referred to by a prior name, Hennig proposes to extinguish the now-ambiguous name and create two new ones. However, he seems to equivocate over whether or not they are new *entities*. [. . .] the issue of 'extinction' of species at cladogenesis is one of the reference of taxonomic names. In short, the 'extinction' is a taxonomic extinction" (Wilkins 2009a, p. 211).[23] Hennig seems to agree when he calls this argument "an argument about words" ("ein Streit um Worte", Hennig 1974, p. 292). Mayr (2000c, p. 164; see also Mayr 1974, p. 110) writes dismissively: "Hennig's suggestion to call the part of a phyletic lineage above a budding point a different species from the part below the budding point is a purely clerical ('bookkeeping') device and biological nonsense". It is indeed easy to ridicule this formalism by pointing out a scenario where a single pair of individuals becomes isolated from a huge population and undergoes rapid morphological divergence, while the parental population does not change at all and still would have to be a "new" species. Also, individual organisms like a hydra budding off another one or human parents having children do not cease to exist after giving rise to these offspring. However, things are not quite that easy. What about vicariant speciation where the two daughter populations are more or less the same size? Would that warrant two new

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[22] This reluctance shows once again that we tend to *think* of species as groups based on similarity and that the evolutionary step from one species to another should include some kind of visible or measurable change in the organisms of the two species. This, however, may not be necessary.

[23] See also Rieppel (2007, p. 377): "For Hennig (1966, in Schlee 1971), this [the extinction of the ancestral species] had to be the case for formal reasons dictated by the relation hierarchy he had adopted from Woodger (1952) and Gregg (1954), not for biological reasons".

species names? After all, in cell division we do not think that the dividing cell remains numerically the same: a mitotic division of the zygote does not result in the zygote and *one* other cell. So, how big must the difference be between the new and the parental population for the latter to keep its name? This is obviously a rhetorical question. Frost and Kluge (1994, p. 271, 272)—who embrace the Evolutionary Species Concept, not any of the cladistically based concepts—write: “When the statement is made that one species is ‘ancestral’ to another, identity (individuality) and diagnosis (an extensional abstraction) are confounded. The only information that can be gleaned from this statement of ‘ancestry’ is descriptive of samples of organismal characteristics, not lineages. That is, the diagnosis (extensional abstraction) of one population is pervasively plesiomorphic with respect to a putatively ‘derivative’ population, whose component organisms have one or more apomorphies. [. . .] Lineages can divide and become multiple lineages, none of which individually share the identity of the ancestor, although they may in aggregate. The view that species can survive lineage partition seems to extend from analogy with organismal bodies surviving gestation and birth. However, the identity of an organism is generally taken as conscious or corporal continuity, something not present in lineages. The analogy from organisms to lineages is not gestation and birth; it is mitosis or schizogony. If one is determined to argue identity of species from analogy with organismal identity, a slime mold would be a much better example than a human”.

Another aspect of surviving stem species is that they would be, by definition, paraphyletic. This is often criticized by those who require also species (and not just supraspecific taxa) to be monophyletic (e.g. Meier and Willmann 2000a). But it is doubtful whether monophyly is applicable at all at the species level (see Sect. 5.6.1), and in any case, stem species, whether they survive taxonomically or not, are necessarily paraphyletic (which is why they were ontologically synonymized by Hennig with the clade that they gave rise to).

From a theoretical point of view, the issue of surviving stem species may be an unsolvable problem, and even some critics admit that the Hennigican Convention may have to apply but that they are not yet convinced (Wiley and Mayden 2000b, p. 156f.). But what about surviving stem species in practice? Willi Hennig himself seems to have been inconsistent, or, as Wiley and Mayden (2000c, p. 205) put it: “It would seem that Hennig-the-theoretician differed from Hennig-the-working-systematist”. And indeed, when discussing the gall wasp (*Stenodiplosis geniculati*) which was introduced from Europe to New Zealand where, following divergence, a new species may be recognized—which would entail a name change in the European stem species—Hennig writes: “Such a statement appears paradoxical to the logical human mind, and obviously no systematist would be prepared [. . .] to give another name to the species that is still called *Stenodiplosis geniculati*” (Hennig 1966, p. 61). Demes and populations, or even just a few individuals, become separated from their parent populations constantly through time and space, making—in theory and under the ontology of the Hennigian Convention—name changes necessary for many if not all species many times (perhaps even many times per day). However, this can be acknowledged without dramatic taxonomic consequences, because the vast majority of these spin-offs will go unnoticed: “Although this implies a startlingly enormous number of ‘smallest’ lineages, even though most of these are likely stillborn, this is no reason to deny their existence. This is the price for not appealing to overall organismal similarity as a measure of lineage identity. However, we think that this price has no particular practical cost [. . .] Geographic range pulses and fragmentations with a frequency more rapid than the development of diagnostic characters are currently beyond our ability to resolve. Therefore they are not a practical issue, inasmuch as they do not touch on naming conventions or on the operations that we use in an attempt to identify lineages” (Frost and Kluge 1994, p. 271f.). The genomic era with its huge increase in resolving power of interpopulational differences will perhaps change this in the near future.

Mishler and Brandon (1987) offer a somewhat idiosyncratic solution to the problem of “ancestral species”. By defining monophyly in terms of a common ancestor (explicitly not an ancestral species!) and its descendants, they hold that species arise from a unit less inclusive than the species level, for example, a local population or a kin group (Mishler and Brandon 1987, p. 409). As a result, they consider the problem of surviving ancestral species solved (or perhaps rather dissolved) because “[n]o such thing exists. Only parts of an original species give rise to new ones”, and paraphyletic ancestral “species” should “be broken up into smaller monophyletic species” (p. 410). Whether that is a feasible approach in practice is, of course, a different question.

The problem of the surviving stem species is therefore first and foremost a theoretical problem, but a theoretical problem that reveals a very important truth. We may find it counterintuitive and in some cases even biologically flawed or outright nonsensical to accept that an ancestral species should cease to exist (even if only taxonomically), but “To claim that one, and not the other, would represent the surviving stem species must be based on some criteria other than phylogenetic relationships”, and “whoever follows Mayr (1974) i[n] his or her contention that ancestral species may survive in a cladogenetic speciation event, or even with the claim that there is no such perfectly symmetrical fission event to be expected in nature, will have to admit that species are individuated not only by their phylogenetic relations, but by additional properties as well” (Rieppel 2007, p. 378).

5.6 Phylogenetic Species Concepts

As explained in Chap. 4, the term Phylogenetic Species Concept is ambiguous, and I only distinguish between two versions, the diagnosability and the monophyly version.[24] I include the diagnosability version based explicitly on apomorphies in

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[24] Davis (1995) distinguishes four different Phylogenetic Species Concepts that, in the terminology of this book, are (1) Hennigian, Cladistic and Internodal Species Concepts; (2) monophyly version of the Phylogenetic Species Concept; (3) diagnosability version of the Phylogenetic Species Concept; and (4) Genealogical Species Concept. There are other classifications, e.g. by Wilkins (2009a), but this latter one is confusing (and inconsistent, if not flawed, I think) as Wilkins mixes up the distinction between diagnosability and monophyly versions and seems to suggest (p. 205ff) that monophyly is not necessarily implied by concepts based on apomorphies.

the monophyly version of the concept (in line with Davis 1995) because the presence of apomorphies establishes a monophylum. This holds under all conditions except perhaps when anagenetic or phyletic speciation is allowed for (different "chronospecies" along an unbranched lineage) in which case consecutive lineage segments can be acknowledged based on the fixation of a character (apomorphic or plesiomorphic), and the concept of monophyly is not applicable in its usual meaning. But even within the diagnosability and monophyly versions of the Phylogenetic Species Concept, there are many variations on a common theme, and a critique of what one author says may not apply to all adherents of the species concepts subsumed under these two names. Most adherents of Phylogenetic Species Concepts have a cladistic background and are often primarily interested in phylogenies, searching for a species concept that provides them with the basic unit for a phylogenetic (cladistic) analysis. However, there are two different schools of cladistics that are usually called process cladistics and transformed or pattern cladistics. While the former (the classical cladistics or phylogenetic systematics of Hennig and Wiley) is explicitly rooted in evolutionary theory, particularly in grouping based on recency of common ancestry, the latter (whose early proponents were in particular Nelson, Platnick and Colin Patterson) goes one step further by denying the need (not the existence!) of any evolutionary process responsible for the hierarchical patterns in nature. Rather, all that it takes is an analysis of character distribution; the resulting pattern (hence the name) gives, according to pattern cladists, a theory-free classification. Synapomorphies on this approach are no longer due to a recent common ancestor but just patterns of character distributions that can be translated into a hierarchy of more and less inclusive groups. This is often mirrored in different ways of the presentation of relationships: process cladists often tend to depict relationships in dichotomous cladograms, i.e. trees of splitting lineages that are interpreted historically, while pattern cladists often show nested hierarchies without any historical "metaphor" as boxes within boxes. The mode of inference is the same but the underlying theory or ontology is different (Rieppel 2014, p. 125). Pattern cladists divorce systematics (classification) from evolutionary theory and even tend to view taxa in systematics as classes with defining properties rather than historically contingent individuals: "For Patterson (1988), the consequence was a theoretical divide in comparative biology. Systematics is about epistemology; it is about the classification of organisms into a hierarchy of sets within sets on the basis of shared derived characters according to some optimality criterion such as parsimony. Evolutionary theory is about ontology; it is about the real world, its furniture, and how it came to be in the course of Earth history. [. . .] And yet the results of systematic investigations are supposed to provide a link between the two realms, epistemology and ontology: the patterns discovered by systematics are to be causally explained by evolutionary theory" (Rieppel 2014, p. 126). The divide between systematics or classification on the one hand and evolutionary theory on the other is often praised by pattern cladists to allow the systematic relationships among organisms to be interpreted as evidence for evolution without being circular. Pattern cladistics is thus in some regard similar to the school of phenetics which also emphasizes the need for theory-free, purely empirical classification. For more details on pattern and process cladistics, see, for example, Ereshefsky (2001, pp. 66–79) and Rieppel (2014) who also offer a nice historical summary of the development of cladistics. The two versions of the Phylogenetic Species Concept that I will discuss have been described also in terms of the two cladistic schools, with the diagnosability concept and its "focus on patterns" being assigned to pattern cladistics and the monophyly concept with its "eye towards processes" as the process cladistics species concept (Ereshefsky 2001, p. 90; this is in line with the classification of Baum and Donoghue 1995 into character-based and history-based species concepts).

5.6.1 *The Monophyly Version of the Phylogenetic Species Concept (mPSC)*

The mPSC regards monophyly as the main characteristic of species—just like for all supraspecific taxa as well. There are, however, differences among adherents of the mPSC(s). While some want species to be the smallest retrievable population or group of populations with apomorphic characters (i.e. a monophylum) (Rosen 1978, 1979; the LITU concept of Pleijel 1999 and Pleijel and Rouse 2000, although avoiding the term species, is similar), others explicitly emphasize that the species rank is assigned based on their being worthy of formal recognition, e.g. due to their role in biological processes: "A species is the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly [...], that is ranked as a species because it is the smallest 'important' lineage deemed worthy of formal recognition, where 'important' refers to the action of those processes that are dominant in producing and maintaining lineages in a particular case" (Mishler and Brandon 1987, p. 406, drawing on earlier publications by Donoghue 1985; Mishler 1985; Mishler and Donoghue 1982).[25] Both versions of the mPSC, that of Rosen and others and that of Mishler, Donoghue and Theriot, have the same *grouping* criterion (monophyly[26]), but the *ranking* criterion (which level of the nested monophyla should be given species rank, i.e. should define the species category) is different. In the first version, it is simply the smallest retrievable monophyletic unit, and in the second, there is an evaluation of relevance or, to put it more explicitly: in order to "avoid naming formal species taxa where they might be ephemeral or temporary (e.g. small, geographically isolated populations) [...] [s]ome judgment of significance is involved" (Mishler and Theriot 2000b). However, Mishler and Theriot stress that this is not a weakness of their mPSC but

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[25] This is an earlier but very similar definition to that given in Chap. 4 by Mishler and Theriot (2000a).

[26] It should be noted that there are different definitions of monophyly. Mishler and Theriot (2000a, p. 47) define it "synchronically, following the 'cut method' of Sober (1988), as all and only descendants of a common ancestor existing in any one slice in time". This synchronic redefinition of monophyly is heavily criticized by Willmann and Meier (2000). A discussion of monophyly is not within the scope of this book, but it should be kept in mind that there are different definitions of it in different species concepts.

common to all species concepts (in Chap. 6 it will be argued that this claim is correct). It should not be forgotten that some adherents of the mPSC (including Mishler) think that the species category does not exist anymore than the supraspecific (and arbitrary) Linnaean categories and that species ranking therefore is for taxonomic and practical convenience rather than to represent a real level in the hierarchy of the Tree of Life (see Sect. 3.6).

Leaving ranking and delimitation decisions for the next chapter, the most contentious issue about any form of the mPSC is the question whether monophyly is applicable to the species level. Many argue that it is not, and I tend to be one of them (see Rieppel 2010 for a detailed discussion). If there is a divide between reticulating tokogenetic relationships on the one hand and strictly hierarchical phylogenetic relationships on the other, then it will be, however fuzzy its boundaries, at and around the species level. Monophyly, however, is a concept that is only meaningfully applicable to strictly hierarchical relationships, which is why Hennig did not apply it at the species level but only for supraspecific groups. Sober (1992, p. 204) agrees with this: "Monophyly is a way of describing *sets* of nodes in a branching process". Branching results in hierarchically arranged groups, while reticulation causes loops and anastomoses, resulting in a network rather than a tree structure. The boundary of the applicability of cladistic methodology lies exactly at the point below which relationships among taxa become nonhierarchical, and this occurs when dichotomous (or, for that matter, polytomous) branching dissolves into anastomosing networks that are connected through sexual reproduction or, more generally, interbreeding (including lateral gene transfer). This is the reason why in intraspecific analyses, for example in phylogeography, very often networks are preferred over tree reconstruction algorithms (e.g. Posada and Crandall 2001). Cladistic methodology (in fact all hierarchical tree reconstruction methodology) therefore hinges on there being no reticulation that dilutes the hierarchical branching pattern. This condition is simply not met at the level that is usually considered relevant in species concepts. Even after the splitting of a single lineage into two, it takes a while until reciprocal monophyly of the daughter lineages is achieved (often via stages of both polyphyly and paraphyly)—under selectively neutral conditions on average $4N_e$ generations with N_e being the genetically effective population size (i.e. the size of an idealized population undergoing the same amount of genetic drift and inbreeding as the population under study) (Avise 2000a, p. 64ff.; Funk and Omland 2003). This is regardless of the fact that there are often discordances between gene (or other character) trees and species trees that can be a serious error source for the analysis of monophyly (e.g. Pamilo and Nei 1988; Maddison 1997; Degnan and Rosenberg 2006, 2009; Avise and Robinson 2008; for a less technical summary, see Zachos 2009).[27] Difficulties in

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[27] It is now well established that the "single hierarchical pattern" postulate (Brower et al. 1996) is wrong. It postulates that, in the absence of homoplasies and if all analyses are correctly performed, each single character that is used for a phylogenetic analysis will yield the same (and correct) phylogeny because there is only one true organismal evolutionary history, signals of which should be present in all characters of the organisms that evolved along this true historical path in the Tree

inferring correct phylogenetic patterns, however, are a practical problem, while the question of the applicability of monophyly is a theoretical one. Below the point where strictly phylogenetic relationships are replaced by primarily tokogenetic relationships, monophyly is not a valid concept anymore. Since the level where speciation occurs and where species exist is around this divide, species concepts based on monophyly may simply be theoretically flawed because species inherently violate the very conditions under which these concepts are applicable.

5.6.2 The Diagnosability Version of the Phylogenetic Species Concept (dPSC)

The second, and probably more influential, version of the Phylogenetic Species Concept is the one based on diagnosability. Two typical definitions of the dPSC are the following:

> "*the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states*" (Wheeler and Platnick 2000a, p. 58); and
>
> "*the smallest population or group of populations within which there is a parental pattern of ancestry and descent and which is diagnosable by unique combinations of character-states*" (Cracraft 1997, p. 329).

The latter definition of Cracraft is a modification of his 1983 definition where, instead of populations, it said "smallest diagnosable cluster of individual organisms". This led to criticisms that family groups or siblings would fulfil the condition of the species category, but the concept was always meant to be applied at the population level. An earlier version of something like the dPSC was also given in the morphological definition by Cronquist (1978, see Chap. 4) according to which species are the smallest distinguishable and persistently distinct groups. Distinguishability, of course, depends on one's methodological capacities, and Cronquist's specification ("distinguishable by ordinary means") is not very helpful.

As already discussed in Chap. 4, it is important to distinguish two kinds of diagnosability. One is based on the fixation of different character states in different lineages; the other is based on whether a unique *combination* of characters makes them diagnosable, none of which has to be unique on its own or whether groups of individuals are diagnosable statistically, that is, by clustering together without overlap. The former I have called qualitative diagnosability, the latter quantitative or statistical diagnosability. Sometimes, authors are not completely clear whether

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of Life. However, just as endoparasites need not show the same branching pattern as their hosts, genes (or other traits) can have different phylogenetic relationships within the organismal tree which is why cladograms actually comprise a distribution of character trees with a variance (aptly termed "cloudogram" by David Cannatella, see Maddison 1997).

they make a distinction here. What matters, however, is how the dPSC is applied in practice when it comes to the description, naming and delimitation of species.

Two of the most ardent theorists championing the dPSC are Quentin Wheeler and Norman Platnick (2000a, b; Platnick and Wheeler 2000). They emphasize that species boundaries, since they are based on diagnosability, are hypotheses (which, of course, holds for all species concepts and scientific statements in general). Quoting from Nelson and Platnick (1981, p. 11), they say: "'The most we can say is that we have not yet been able to differentiate species within the sample' that we hypothesize to be a single species" (Wheeler and Platnick 2000a, p. 59). Importantly, they distinguish between traits and characters (which are otherwise often used synonymously). Traits in their terminology are properties that are variable within species, while characters are only variable between species but fixed within them, and they accept the tokogeny/phylogeny divide as the level corresponding to the species: "Below this line, populations are characterized by variable traits. Above this line, species and monophyletic clades are characterized by constantly distributed characters" (Wheeler and Platnick 2000a, p. 58, caption to Fig. 5.1; see also Nixon and Wheeler 1990).[28] Accordingly, they hold that monophyly is not applicable to species. They also emphasize that apomorphies are irrelevant for species recognition. To them, "[s]peciation is marked by character transformation which in turn occurs "through the 'extinction' of ancestral polymorphism" (Wheeler and Platnick 2000a, p. 59). However, if each of two alternative states of an ancestral polymorphism become fixed in the two daughter species after lineage sundering, neither of the two is more apomorphic than the other compared to the ancestral species (p. 59f.). Since to Wheeler and Platnick speciation, the origin of a new species, is synonymous with the transformation of a trait into a character, i.e. the extinction of within-population polymorphism, every fixation event marks the birth of a new species, regardless of the processes leading to this fixation event (isolation, vicariance, sympatric divergence; see Fig. 5.3 in Wheeler and Platnick 2000a). This independence is viewed as an advantage of their concept by the authors. Rather than accepting a grey area during speciation (see Fig. 5.2 in this book), on this view, "[t]he moment of speciation is, in theory, precise and corresponds to the death [or emigration, one might add] of the last individual that maintained polymorphism within a population" (Wheeler and Platnick 2000a, p. 59). Of course, then, as soon as a de novo mutation or immigrating individual reintroduces the lost variant into the population, the speciation turns out to be none or reversed (see below). Most notably, speciation does not require lineage splitting; Wheeler and Platnick also accept phyletic or anagenetic speciation: every time a polymorphism disappears within a single population lineage and a trait becomes a character as a result, a new species arises according to this logic. The result is the

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[28] It has been argued that it is impossible to determine with certainty whether characters are truly fixed with finite sample sizes and that a nonzero cut-off criterion may be more realistic (Wiens and Servedio 2000). However, this is an operational argument and does not preclude diagnosability to be viewed as a hypothesis given present knowledge (and sample sizes analysed).

fixation-based acceptance of consecutive chronospecies along a single lineage. This does not sit well with the notion of species being historical individuals and has, expectedly and (I think) legitimately, been criticized: “Evolution and systematics come together when species are directly related to cladogenesis and other kinds of speciation. They never make contact when we allow the arbitrary subdivision of a single continuous tokogenetic array [...] just because an evolutionary novelty becomes fixed (i.e. traits become characters; Wheeler and Nixon 1990) or because we cannot imagine doing any better (Simpson 1961)” (Wiley and Mayden 2000a, p. 88). Similarly, Wiley and Mayden, in their counterpoint chapter of the same book (2000b, p. 149), say “Divorcing binominals from cladogenesis destroys the distinction between tokogeny (nonhierarchical descent) and phylogeny (hierarchical descent). [. . .] Thus, the application of a binominal does not represent an acknowledgment of the transition between tokogenetic and phylogenetic relationships”. It has to be emphasized, though, that other adherents of the dPSC do not embrace phyletic speciation but reject this as an arbitrary subdivision of a historical individual (Eldredge and Cracraft 1980, p. 114, Cracraft 1987).

In practice, the dPSC has recently been applied more often—there seems to have been a paradigmatic shift from the Biological Species Concept to the (d)PSC— and its consequences in mammalian taxonomy have resulted in an intense debate on its merits and/or shortcomings (Isaac et al. 2004; Meiri and Mace 2007; Frankham et al. 2012; Gippoliti and Groves 2012; Gippoliti et al. 2013; Groves 2012, 2013, 2014; Gutiérrez and Helgen 2013; Heller et al. 2013, 2014; Zachos and Lovari 2013; Zachos et al. 2013a, b; Cotterill et al. 2014; Rosenberger 2014; Zachos 2015[29]). This debate was triggered by an increase in the number of acknowledged species in primates, which led Isaac et al. (2004) to coin the term “taxonomic inflation”[30] (see Groves 2014 for a rejoinder)—and later by the publication of the book on ungulate taxonomy by Groves and Grubb (2011) whose taxonomy was subsequently adopted for the ungulate volume within the *Handbook of the Mammals of the World* (Groves and Leslie 2011) and which increased the number of bovid species (wild cattle, antelope, goats, sheep) from 143 in the most recent edition of the taxonomic reference work for mammals (Grubb 2005) to 279. Groves and Grubb (2011) split the red deer/wapiti complex, usually conceived of as comprising two or even a single species (*Cervus elaphus* and *C. canadensis*, respectively[31]), into 12 species, and the klipspringer (*Oreotragus oreotragus*), a

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[29] While including theoretical arguments, these publications are more practical than many works cited earlier in that they deal with evolutionary, taxonomic and conservation biological practice.

[30] Fujita et al. (2012, p. 480f.) define taxonomic inflation as “the artificial increase in the number of species in a group resulting from elevation of geographical variants (often recognized taxonomically as subspecies) to species status. This typically arises when using diagnostic characters regardless of their significance or type under the phylogenetic species concept (morphological or molecular)”.

[31] Mattioli (2011) acknowledges three species, *C. elaphus*, *C. canadensis* and the Central Asian *C. wallichii*, still four times less than Groves and Grubb.

small African antelope, was split into 11 species.[32] Groves' and Grubb's monograph is based on an impressive data set collected over decades, and this alone makes it stand out. But the taxonomic conclusions or rather the underlying rationale is doubtful. The basic approach is multivariate analysis (ideally discriminant analysis) of morphometric data: "As long as sample sizes are large enough [which is by no means always the case, see the klipspringer example], the ideal is to compare different samples of restricted geographic origin with each other, aggregating those which turn out not to be discrete. Eventually, a picture is arrived at in which two or more of these aggregations may remain, and, if they are discrete and there is morphometric space between them, they then answer to the requirements of the [d]PSC. If no discrete groups remain, then there is no morphometric evidence for different species" (Groves and Grubb 2011, p. 5). Diagnosability is thus based on the lack of overlap in morphospace or, more generally, character space. At least some of the adherents of the dPSC explicitly conceive of their approach as working in the framework of Mayden's (1997) hierarchy of species concepts or de Queiroz's (1998) General Lineage Species Concept: "The ESC [Evolutionary Species Concept] frames operations employing the [d]PSC to compare diagnostic characters to test whether or not candidate populations represent distinct lineages" (Cotterill et al. 2014, p. 820f.); "[t]he [d]PSC (or, better, in de Queiroz's clarification, the phylogenetic or diagnosability criterion for species delimitation") (Groves 2014, p. 31). The term "diagnostic characters" in the first quotation is somewhat ambiguous when multivariate analyses are performed on morphometric data because, strictly speaking, there are no diagnostic characters as such but rather a combination of values for continuous traits that makes a group of organisms diagnosably distinct (quantitative or statistical diagnosability), but this is not relevant for the present discussion. These authors thus embrace the notion of species as lineages and consider the dPSC as *the* appropriate species identification criterion (as opposed to Mayden and de Queiroz who regard the secondary identification criteria as complementary and similarly appropriate). What, if anything, is wrong with this approach? It has often been bemoaned that it leads to a huge increase in species numbers. Agapow et al. (2004) have estimated (conservatively) that the application of Phylogenetic Species Concepts will lead to a minimum increase of species numbers by at least 48.7 % across a variety of animal, plant and fungal taxa, although others have concluded that this may be taxon-dependent and not so dramatic for beetles and spiders (Wheeler and Platnick 2000a, p. 60). But let us suppose that the dPSC would dramatically multiply species numbers. The answer of its adherents is "so what? If the goal of distinguishing species is to thereby recognize the end-products of evolution, should we seek to suppress naming large numbers of species where large numbers of differentiated end-products exist?" (Wheeler and Platnick 2000a, p. 60; see also, for example,

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[32] The taxonomic revision of the klipspringer was additionally criticized because of the very low sample sizes (often < 5) on which it is based. This criticism, however, is very different from the general criticisms of the dPSC.

Groves 2012, 2013 for a similar view). And indeed, this answer would be fully legitimate if the criticism aimed at species *numbers* alone. However, it doesn't. What is implied by the inflation of species numbers is a shift in the *nature* of the groupings that are to be classified. As already stated, the dPSC, like every other species concept, is based on biological realities (diagnostic differences are after all very real). However, given high enough resolution of the characters studied, even the smallest groups of related organisms become diagnosably distinct (one need only think of genomic data sets to appreciate this). Since the dPSC explicitly and wisely limits the lower boundary for species status to the population level, species and populations effectively become synonyms, and the question "What is a species?" is replaced by "What is a population?" (see Hey 2001a, p. 157; Mishler and Theriot 2000b, p. 130; and Heller et al. 2014 for the same conclusion).[33] The dPSC, according to its adherents, trumps other species concepts or identification criteria by its being testable in a straightforward manner ("The [d]PSC depends on evidence, not on inference", Groves 2013, p. 7), but this comes at a price: equating the species level with that of the population, and this is the reason for the increase in species numbers inherent to the dPSC. Again, numbers of species are in themselves no argument against an underlying species concept, but the properties thus assigned to species or, rather, the lack thereof when ephemeral and/or superficial entities are given species rank certainly is. Taking the dPSC to a molecular extreme, tigers (*Panthera tigris*) have been split into two species based on three diagnostic base pairs in sequences of the mitochondrial cytochrome b gene (Sumatran tigers *Panthera sumatrae* and the rest, Cracraft et al. 1998). Based on craniometric diagnosability Mazák and Groves (2006) even recognized three tiger species (Sumatran tigers, extinct Javan tigers *Panthera sondaica* and the rest). This has been criticized as diluting the relevance of the species category (Zachos et al. 2013a)—as in economy in taxonomy, too, inflation leads to devaluation. But the logic of this approach does not stop here as has been emphasized by Zachos and Lovari (2013): genetic drift in small isolated tiger populations in India has already led to the fixation of mitochondrial haplotypes in some of them (Sharma et al. 2011), and soon the majority of these populations may be diagnosably distinct from each other. The fact that tigers are dwindling towards extinction will thus cause a multitude of new tiger "species" before they all vanish.[34] While there is of course nothing wrong with this view from a logical perspective, it is doubtful whether it represents anything that is biologically meaningful. And of course, as soon as there is a mutation in one of the haplotypes, diagnosability might be lost, so

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[33] It should be added here that this is in line with some phylogeneticists, e.g. Rosen (1978, p. 176f.), who holds that the population is the "unit of evolutionary significance", not the species which, as traditionally conceived, is a "unit of taxonomic convenience" (see Bunge 1981 for a similar view). Rosen's concept is included with the mPSC because it is based on apomorphies which delineate monophyla, but with regard to the hierarchical level of interest, that does not make a difference here.

[34] Avise (2000b) makes the exact same argument with respect to tiger beetles whose species numbers will also be multiplied due to habitat fragmentation.

that either the two former diagnostic species would have to be merged again (something like de-speciation or reverse speciation, see Fig. 2 in Zachos and Lovari 2013), or it would have to be concluded that they never were distinct species in the first place.

However, there is another serious issue to be considered here. The dPSC, whether it is interpreted in the hierarchical framework of Mayden and de Queiroz or not, is often praised as the only truly objective way of delimiting species (Wheeler and Platnick 2000a; Groves 2012, 2013; Cotterill et al. 2014), and more specifically, it is considered to be standing out because it can deal with allopatric populations whose species status is determined not based on inference but evidence; in contrast, "[a]dherence to reproductive isolation, reciprocal monophyly or population fitness as preeminent criteria for specieshood *invariably* overlooks lineages represented by allopatric populations" (Cotterill et al. 2014, p. 825). But is it true? Is the dPSC really exceptional in its testability and its capability of objectively assessing the status of allopatric populations? In the next chapter, I will argue that truly non-arbitrary species delimitation is a myth that it is impossible in a world of fuzzy boundaries—and this holds regardless which species concept is applied, including the dPSC. In a previous publication (Zachos 2015), I have argued that species delimitation as practised and defended by, for instance, Groves and Grubb (2011), Mazák and Groves (2006) and Cotterill et al. (2014), is inconsistent. They explicitly consider the dPSC as a species criterion in the framework of the Evolutionary or General Lineage Species Concepts (see quotations above), so diagnosability is a *proxy for species status, not what makes a species*. They use diagnosability to detect population-level lineages. But then, if there is evidence for a population-level lineage in the absence of diagnosability, that lineage would have to be a species, too. This is the case for all allopatric populations. In the absence of gene flow, they are by definition distinct population-level lineages! Consequently, species status (distinct population-level lineage) has been found by means of another criterion, and diagnosability is thus only a sufficient but not a necessary condition for species status. If one insists on diagnosability nonetheless, it is not a criterion anymore but more like a definiens of species, which is in contrast to claims of working under the rationale of the Evolutionary and/or General Lineage Species Concepts. This is exactly what Groves and Grubb (2011) and other adherents of the dPSC do, however. They accept, for example, the island population of red deer on Corsica and Sardinia as a distinct species (*Cervus corsicanus*) but fail to acknowledge other island populations of red deer at the species level (e.g. red deer on the British Isles or introduced red deer in New Zealand), on the grounds that they are not diagnosably distinct. They even combine the Corsican red deer with the completely isolated North African Barbary red deer into one species because the two, although very obviously being two separate population-level lineages, fail the diagnosability test. So, either they are being inconsistent here or diagnosability is more than a species identification criterion. It would then not be a proxy for population-level lineages, but a test for *diagnosably distinct* population-level lineages. However, then it would not be fundamentally different from any other species concept that acknowledges population-level lineages as species when and if a certain threshold criterion is met, e.g. reciprocal monophyly or intersterility. This, at the very least, would mean that the prominent position that is claimed for the dPSC by its adherents is doubtful. For it, just like for all other secondary species concepts or criteria, we then must conclude: an arbitrary cut-off criterion that can be measured objectively is *not* the same as an objective delimitation criterion! This line of argumentation will be picked up again in Chap. 6.

5.7 Prokaryotic Species and Species Concepts[35]

The two most important *taxonomic* issues of the species problem are (1) how to individuate the continuous Tree of Life into objectively real historical entities or individuals (species taxa) and (2) to define a common taxonomic level that makes all species taxa directly comparable because they are all part of the same biologically meaningful class of objects, the species category. The first point pertains to the grouping of organisms and the second to the ranking of these groups. Prokaryotic organisms challenge the feasibility of both these issues, much more so than eukaryotes. This is a serious matter, since, although we usually think of animals or plants when we think of species (unless we are microbiologists), most living organisms on earth are prokaryotes. Still, while more than 1.5 million eukaryotic species have been described, the number of taxonomically acknowledged species of bacteria and archaea is only about 5000 (Staley 2006). Our perspective is therefore—inexcusably from a scientific point of view, many might want to add—biased towards the macrocosm in which we live and to which our sensory organs are adapted.

It is well known that in prokaryotes, species boundaries are even fuzzier than in other taxonomic groups, and, therefore, the discrepancy between T species and E species will be on average larger, sometimes very much so. In fact, probably nowhere across the Tree of Life will this discrepancy be nearly as large as in the prokaryotic world. I will not discuss the debate on prokaryotic species in detail here but instead only give an overview of the topic. More detailed information from within the microbiological community can be found in Vandamme et al. (1996),

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[35] I will not discuss species concepts for viruses, which are very different from other organisms and are usually not even considered living beings. One concept for viruses is the quasispecies of Eigen and colleagues (see Sect. 5.1). For a short review of viral species, see Van Regenmortel (1997) and Peterson (2014). The latter argues for a lineage-based species approach to viral taxonomy to overcome classifications for mere convenience. The lineage approach is already partly implemented in the International Code of Virus Classification and Nomenclature according to which the viral species category is defined as “a monophyletic group of viruses whose properties can be distinguished from those of other species by multiple criteria. [...] These criteria may include, but are not limited to, natural and experimental host range, cell and tissue tropism, pathogenicity, vector specificity, antigenicity, and the degree of relatedness of their genomes or genes” (Adams et al. 2013, p. 2636).

Embley and Stackebrandt (1997), Goodfellow et al. (1997), Lan and Reeves (2001), Rosselló-Mora and Amann (2001), Cohan (2002), Stackebrandt et al. (2002), Gevers et al. (2005), Doolittle and Papke (2006), Achtman and Wagner (2008) and Doolittle and Zhaxybayeva (2009); Ereshefsky (2010c) provides a succinct theoretical discussion. Much of the information presented here is taken from these publications.

Operationally, bacterial species are usually "defined" based on DNA–DNA hybridization. A species is a group of strains that shows 70 % or more homology of the genome in hybridization assays, i.e. 70 % or greater DNA–DNA relatedness, and 5 °C or less difference in melting temperature between homologous and heterologous hybrids. This is an empirical but arbitrary threshold value. The species category is thus a taxonomic convenience and not based on any kind of underlying biological theory. In practice, one of the problems with this approach is that it is not always transitive, i.e. if strains A and B turn out to meet the criterion of distinct species status and the same is true for B and C, it does not follow that A and C will also meet it (Achtman and Wagner 2008). Another cut-off criterion is based on sequences of 16s rRNA. The threshold value here is usually given as 97 % sequence identity (Embley and Stackebrandt 1997 give 98 %, Achtman and Wagner 98.7 %) below which different species status is assigned because it has been shown that this threshold correlates well with the 70 % DNA–DNA hybridization value. Similar to other taxonomic groups, there have been appeals to integrate all lines of evidence from different realms (genotypic, phenotypic, phylogenetic) into a combined or "polyphasic taxonomy" (often also called "integrative taxonomy") to arrive at some kind of consensus classification (Vandamme et al. 1996).

Approaches to defining the species category and delimiting species in prokaryotes are usually recombination-based, ecological or phylogenetic. The recombination approach is based on a kind of microbial equivalent of the Biological Species Concept (Dykhuizen and Green 1991, but arguably many other species concepts would be in accordance with this as well) in focusing on a prokaryotic gene pool—all bacteria belong to the same species whose genomes can recombine. A modified version of this application of the Biological Species Concept to prokaryotes based on core genes (see below) is also promoted by Lan and Reeves (2001).

The ecological approach is based on so-called ecotypes which, according to Cohan (2002), are the equivalent to species in eukaryotes in that they are cohesive units that have diverged irreversibly and are ecologically distinct. What is usually called a species in microbiology is more like a genus in eukaryotes and will contain more than one ecotype. "An ecotype is a set of strains using the same or similar ecological resources, such that an adaptive mutant from within the ecotype out-competes to extinction all other strains of the same ecotype; an adaptive mutant does not, however, drive to extinction strains from other ecotypes" (Cohan 2002, p. 466f.). Periodic purifying and stabilizing selection will keep the ecotype adapted to its niche such that "[a] species [*sensu* ecotype] in the bacterial world may be understood as an evolutionary lineage bound together by ecotype-specific periodic selection" (ibidem, p. 467). Interestingly, Cohan also characterizes ecotypes as "evolutionary lineages that are irreversibly separate, each with its own evolutionary tendencies and historical fate" (p. 467) and with this quote and the citations that come with it makes explicit reference to the Evolutionary and General Lineage Species Concepts of Simpson, Wiley and de Queiroz. A microbial species concept based on de Queiroz's metapopulation lineage concept is also favoured by Achtman and Wagner (2008).

Rosselló-Mora and Amann (2001) present a (partly) phylogenetic approach that they call phylo-phenetic. According to this Phylo-Phenetic Species Concept, a species is "*a monophyletic and genomically coherent cluster of individual organisms that show a high degree of overall similarity with respect to many independent characteristics, and is diagnosable by a discriminative phenotypic property*" (Rosselló-Mora and Amann 2001, p. 59, italics in the original). This definition combines elements of both the diagnosability and the monophyly versions of the Phylogenetic Species Concept with the Genotypic Cluster and Phenetic Species Concepts (see Chap. 4).

In principle, all problems with these kinds of species concepts that apply to eukaryotes apply to prokaryotes as well. There is, however, one issue that exacerbates these problems in the microbial world: lateral gene transfer (LGT), also called horizontal gene transfer (HGT). It occurs in eukaryotes as well sometimes, but in prokaryotes it is rampant (e.g. Bapteste and Boucher 2008; Soucy et al. 2015). Lateral gene transfer is the transfer of genetic material between organisms by mechanisms other than (vertical) reproduction, e.g. through bacterial conjugation, the introduction and incorporation of foreign genetic material through the cell membrane (transformation) or virally mediated introduction of genetic material in bacteria (transduction). Approaches like multilocus sequence analysis (MLSA, Gevers et al. 2005) yield sequence clusters, but how exactly these clusters are to be interpreted taxonomically is a difficult question. Discordances between gene and species trees are common also in eukaryotes, but in prokaryotes the signal of gene trees is so ambiguous because the gene pool from which the phylogenetic markers are drawn is so different from that in eukaryotes: LGT might occur, in principle, across the whole prokaryotic world. This is accounted for by the concept of the microbial "pan-genome" (Medini et al. 2005; Tettelin et al. 2005). Analyses have shown that there is something called a "core genome" that is the "pool of genes shared by all the strains of the same bacterial species" and a "dispensable genome" (also called accessory genome, Soucy et al. 2015) that comprises the "pool of genes present in some—but not all—strains of the same bacterial species". The pan-genome is then simply the "global gene repertoire of a bacterial species: core genome + dispensable genome" (Medini et al. 2005, p. 590).[36] The core genome usually includes genes for basic cellular function ("housekeeping genes", Lan and Reeves 2001), but genes from the dispensable genome can be introduced by LGT and convey an adaptive advantage (Achtman and Wagner 2008). Pan-genomes can be closed (when genomes of a few individuals are enough to yield the pan-genome)

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[36] A similar distinction between "core genes" and "auxiliary genes" was introduced earlier by Lan and Reeves (2000) in their "species genome concept".

or open in which case every new analysed genome will yield new auxiliary genes so that the core genome only represents a small fraction of the pan-genome (Tettelin et al. 2005). To reduce problems in phylogenetic analysis, it has been suggested to base species status only on data derived from the core genome (Lan and Reeves 2001). However, rampant LGT will effectively turn the Tree of Life into a "web of life", and therefore, the inference of phylogenetic relationships and the detection of phylogenetic lineages in microbiology as a means to clarify species status may be doomed: "Useful as such trees [based on core genomes] may be, we must realize that they will not represent the true intergenomic relationships in recombinogenic groups, which will be reticulate, not tree-like—nor will they describe the evolutionary behavior of the non-core part of the pangenome of any species, which may be much larger than the core" (Doolittle and Papke 2006, p. 116.6). LGT has been considered to render the problem of species concepts in microbiology unsolvable because it makes "evolution reticulate and organismal history chimeric" so that notions of lineages, at least at the level of organisms, are not applicable anymore—"reticulate evolution through lateral gene transfer (LGT) is the elephant in the room of prokaryotic systematics" (Doolittle and Zhaxybayeva 2009, p. 745). In conclusion, these authors predict that the focus will shift towards the analysis of processes, decoupled from taxonomic concepts: "We anticipate that as metagenomics and the sophisticated computational environment needed to understand and represent metagenomics data evolve, the word [species] will disappear from scientific literature" (p. 754). Similarly, Bapteste and Boucher (2008) advocate a shift away from notions of a single basic natural evolutionary group (the species) towards "composite evolutionary units". An evolutionary unit in their view is an "integrated association of lower level elements that can be replicated and are held together by some biological mechanism" (Bapteste and Boucher 2008, p. 203). Because LGT results in different parts of organisms having different evolutionary histories and therefore belonging to different "species" (making the organism a chimaera), the notion of species should be replaced with that of evolutionary units that exist at different organizational levels: from parts of organisms to microbial communities. "[S]tudies on LGT strongly suggest the existence of multiple levels of selection and the presence of many biological 'individualities' in complex interactions in the microbial world. We thus argue for a richer view of biodiversity, comprising more evolutionary units than the mere 'species' and 'genes' generally considered in traditional phylogenetics, and thus more natural groups to classify" (p. 204). Therefore, "the question of the origin of a microbe [as relevant for species status] is superseded by (1) the question of the origins of its many constitutive elements (the various smaller evolutionary units of which it is made) and (2) the question of whether this organism might itself belong to larger composite evolutionary units" (p. 204). These composite evolutionary units "rely on parts which might have different origins, some global biological process being responsible for their association while selection is acting on the emerging higher-level phenotype" (p. 204). While maybe unfamiliar, the authors argue that this approach will represent evolutionary processes more realistically than the traditional lineage-based notion of species that have a single origin.

It is worth noting that a twofold pluralism is lurking in bacterial systematics: (1) the same organisms can be sorted into different species based on different species concepts (e.g. based on recombination, gene pools, ecology or phylogeny), but (2) the same organisms can also be sorted into different species based on the same species concepts: if, for example, different parts of an organism's genome have different evolutionary histories, phylogeny-based approaches will classify these parts into different species. Ereshefsky (2010c) calls these two kinds of pluralism inter-approach (1) and intra-approach (2) pluralism. While intra-approach pluralism can also apply in eukaryotes when there are discordances between gene and species trees, in prokaryotes, particularly those with an open pan-genome or at least a relatively small core genome, it will be the rule rather than the exception. LGT thus exacerbates the search for a unifying species concept in microbes. Eventually bacterial species may turn out to be little more than T species that exist for our convenience and not for their underlying biological relevance or meaningfulness. Microbial species taxa would then be more like class concepts (with the defining property of having, for example, 97 % or more identity at the 16s rRNA sequence) than like actual historical individuals.[37] The overall consequence would then be that "there is no principled way in which questions about prokaryotic species, such as how many there are, how large their populations are, or how globally they are distributed, can be answered" (Doolittle and Zhaxybayeva 2009, p. 744). And while this "would be a disappointment perhaps [. . .] it is no excuse for forcing a conceptual straitjacket on unruly data" (p. 754). In fact, this may hold not only for the microbial world but perhaps for all of life, even for eukaryotic species most of which are conceived of as individuals much more easily than prokaryotes. This will be further discussed in Chap. 7.

5.8 Species as Process or as Pattern Entities?

Theodosius Dobzhansky's "species as a stage in a process" quote and Ernst Mayr's objection to it (species as the result of a process) have been briefly discussed in Sect. 1.4. This hints at another debate: while nobody doubts that speciation is a process (in the meaning of something occurring *through* time) and that species can in a way be considered a result of such a process, there is disagreement over whether species concepts should be based on processes or just patterns regardless of the processes that have brought them about. "On the view of species as pattern entities, a species is purely an effect or result of causal processes in nature; those processes themselves are not part of what a species is. On the view of species as process entities, on

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[37] There are exceptions. *Buchnera aphidicola*, an obligate endosymbiont of aphids (plant lice), has not undergone lateral gene transfer (or indeed any genomic rearrangements) in more than 50 million years (Tamas et al. 2002) and thus is as good a single historical individual or lineage as any species.

the other hand, the causal processes are indeed part of what a species is" (Stamos 2003, p. 321). Stamos also explains why, in his view, the pattern-based approach is superior to the process-based notion: "process species concepts [...] are based on only one or a few of the causal processes or mechanisms involved in evolution, while pattern species concepts [...] are based on the end-products or effects of those causal processes. Process species concepts have the liability that they tend to exclude certain kinds of organisms from species membership, so that certain kinds of biologists are left out in the cold. The result is that many biologists either turn to other species concepts or embrace a sort of species pluralism. Pattern species concepts, on the other hand, are not theory dependent as to the different kinds of causal mechanisms and processes in evolution and are accordingly potential candidates for a truly universal species concept" (Stamos 2003, p. 26). Following Cracraft (1989), Stamos (2003, p. 26, 320) gives as process concept examples the Biological (Mayr), Recognition (Paterson), Ecological (Van Valen) and Evolutionary (Wiley) Species Concepts and as examples of pattern concepts the Phenetic (Sneath and Sokal), Morphological (Cronquist) and Phylogenetic Species Concepts (diagnosability version, Cracraft). Templeton's Cohesion Species Concept he considers as a particular case within the process concepts because it is "based on many rather than on one or a few evolutionary processes" (Stamos 2003, p. 321). A very different view of the Evolutionary Species Concept (and the General Lineage Concept), rejected by Stamos, was presented in Sect. 5.2 where it is argued that it is a maximally general notion of species rather than a limited one when compared to pattern concepts. In addition, I do not think that the argument of more general applicability of pattern concepts is necessarily convincing. While perhaps true, it remains to be shown that this kind of generality is actually the one we mean when saying that a species concept applicable to all organisms under all circumstances is what we are ideally aiming for. As desirable as a truly general species concept is, it should not deceive us into thinking that entities bearing the same name ("species") are the same and thus objectively comparable when in reality they are not. Sexual and asexual organisms, for example, might just not fit into the same kind of species concept, such that the same name does not denote the same kind of entity. Although the debate is still open, the one-fits-all species concept may eventually well turn out to be taxonomy's Holy Grail, and concepts embracing or claiming to embrace all taxa and situations might only be masking the differences between the entities covered by them, thus introducing a serious apples-and-oranges problem into ecology, biodiversity research and evolutionary biology (see Chap. 7).

5.9 Superspecies, Subspecies and Evolutionarily Significant Units

Apart from the species level, there are other taxonomic levels that are often discussed when it comes to the species problem. I will briefly discuss the superspecies concept and then, a little more detailedly, infraspecific categories, in particular the subspecies and an alternative concept, Evolutionary Significant Units or ESUs.

The superspecies concept (Mayr 1931; Amadon 1966; Mallet 2001b) goes back to the German literature of the early twentieth century when Kleinschmidt's *Formenkreis* (ring or circle of forms) was substituted by Rensch's terms *Rassenkreis* (*circle of races*) and *Artenkreis* (*circle of species*), with the former being equivalent to species and the latter to a group of related species replacing each other geographically. Ernst Mayr then translated these terms into English as polytypic species (equivalent to *Rassenkreis*) and superspecies (equivalent to *Artenkreis*) and combined them into what he called Biological Species Concept (Mallet 2001b). The component parts of a superspecies were named semispecies. This term originally denoted "good" but similar species, but in line with the literal meaning of the term (semi = half), it has increasingly been used to denote borderline cases between subspecies and full species, i.e. populations that are considered to have acquired some but not all characteristics of distinct species.[38] Amadon (1966) suggests to restrict the term semispecies to the latter meaning and call the "good" species that form a superspecies allospecies and mark them with square parentheses such that *Accipiter* [*gentilis*] *gentilis*, *Accipiter* [*gentilis*] *melanoleucus* and *Accipiter* [*gentilis*] *meyerianus* are a way of expressing that the goshawk *Accipiter gentilis* is a superspecies and that *A. gentilis*, *A. melanoleucus* and *A. meyerianus* are allospecies within that superspecies. This concept has been included in the guidelines for assigning species rank of the British Ornithologists' Union (BOU) (Helbig et al. 2002), in a slightly modified version. The superspecies concept here is an attempt at distinguishing between different levels of evolutionary independence of population-level lineages. The authors embrace the hierarchy of species concepts in that they consider the Evolutionary and/or General Lineage Concepts as the underlying ontological species concept and view the other species concepts as species identification criteria. By introducing super-, allo- and semispecies, they increase the categorical arsenal to describe lineage divergence. A "normal" species would then be one that is well differentiated from its closest relatives so that there is little doubt as to its being an independent evolutionary lineage. A superspecies, on the other hand, is a monophyletic group of allospecies and/or semispecies that are less differentiated. Allospecies are geographically separated, while semispecies are connected by a stable hybrid zone, and they are

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[38] Mayr (1969) gives both meanings of the term in his glossary; in the glossary of the second edition (Mayr and Ashlock 1991), semispecies are only defined as borderline cases between subspecies and full species.

marked by Amadon's square bracket nomenclature. A stable hybrid zone is in itself considered to be evidence of the two taxa being largely independent. Helbig et al. (2002, p. 522) conclude that situations like these "always indicate a substantial restriction of gene flow, e.g. Carrion Crow *Corvus corone* and Hooded Crow *C. cornix*". That this prime example of semispecies according to the guidelines of the BOU turns out to be much less restricted in gene flow than previously assumed (see Sect. 5.4) shows that the superspecies approach, even though more refined than a simple binary one species vs two species option, is still far too coarse to adequately capture the complex and continuous process of lineage divergence.

A much more common issue than that of superspecies is that of infraspecific categories, particularly the subspecies.[39] Definitions of this rank include:

> "*A subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species*" (Mayr 1969, p. 41); and
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> "*subspecies are groups of actually or potentially interbreeding populations phylogenetically distinguishable from, but reproductively compatible with, other such groups. Importantly, the evidence for phylogenetic distinction must normally come from the concordant distributions of multiple, independent, genetically based traits*" (Avise and Ball 1990, p. 59f.).

The latter definition is the subspecific equivalent of the Genealogical Concordance Species Concept of the same authors, and they agree that subspecies are normally allopatric, but they put emphasis on subspecies being phylogenetically, not just phenotypically, distinguishable. The first is the classical definition sensu Mayr. Mayr acknowledges the basic problem with diagnosability (whether in the context of the species or the subspecies category): "Every local population is slightly different from every other local population, and the presence of these differences can be established through sufficiently sensitive measurements and statistics. It would be absurd and would lead to nomenclatural chaos if each such population were given the formal trinominal name that is customary for subspecies. Therefore, subspecies are to be named only if they differ 'taxonomically', that is, by sufficient diagnostic morphological characters" (Mayr 1969, p. 42). This introduces a level of arbitrariness, of course. The most widely used threshold for subspecific designation, which in itself is an arbitrary cut-off criterion but allows for standardized and comparable decisions, is the "75 % rule" (Amadon 1949). It means that "subspecies A is recognized taxonomically if, and only if, $\geq$75 % of the individuals in group A lie outside 99 % of the range of variation of group B for the character or set of characters under consideration" (Patten 2015). This arbitrariness, however, primarily pertains to the subspecies *category*. Just like there is a fundamental difference between the species category and the species taxon, there is one between category and taxon at the subspecific level, and one has to distinguish between the

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[39] I will not discuss the variety of infraspecific labels that are available in botany and microbiology, such as variety, form, ecovar, geovar, etc. In principle, the theoretical issues pertaining to the subspecies apply to them as well.

reality of subspecies taxa and the reality of the subspecies category. If subspecies taxa represent evolutionarily and/or phylogenetically distinct portions of a species, i.e. lineages within the species level of lineages,[40] then they can be considered real (in the sense of extramental reality), but classifying a number of these portions at the same level (subspecies category) almost certainly neglects the intraspecific hierarchical pattern among them. In other words, what is given the same rank is hierarchically at different ranks because some of the subspecies will be more closely related than others, resulting in a nested pattern. This is the same problem as with higher Linnaean categories when, for example, extant mammals are subdivided into 18–20 “orders” which suggests that they are all at the same hierarchical level, which is of course not the case. The comparability of different subspecies taxa (that they really refer not only to biological entities but to the *same kind* of biological entities) and thus the reality of the subspecies category are highly doubtful, even more so than that of the species category. That subspecies *taxa*, however, can represent real biological entities has been shown for a number of organisms. Luo et al. (2004) found that taxonomically acknowledged tiger subspecies were distinct genetic groups (indeed, they found that one such group included two well-differentiated subgroups so that they named an additional subspecies, the Malayan tiger *Panthera tigris jacksoni*, formerly part of the Indochinese tiger *P. t. corbetti*). Similarly, within red deer, there are divergent populations that represent distinct and unique phenotypes and genetic lineages, e.g. the Tyrrhenian red deer from Sardinia and Corsica, the North African Barbary red deer in Algeria and Tunisia and the last autochthonous Italian mainland red deer in Mesola in the Po delta region (Zachos and Hartl 2011 and references therein). While the first two had long been acknowledged as subspecies (*Cervus elaphus corsicanus* and *C. e. barbarus*, respectively), the Mesola deer were until recently lumped with the majority of European mainland red deer into *C. e. hippelaphus*, although their degree of distinctness is comparable to that of the Tyrrhenian and the Barbary red deer. Although the authors were aware that the subspecies category is not objective, Zachos et al. (2014) assigned subspecific status to the Mesola red deer (*C. e. italicus*) because they represent an objective entity within the species red deer that, since subspecies classification is being practised, deserves to be taxonomically acknowledged just as much as the other two subspecies, particularly because an official taxonomic name has corollaries for conservation and management (see Sect. 7.1). But if subspecies taxa fulfil the conditions of biological entities, the question of course arises: why not assign them species rank? Why introduce a level

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[40] In how far this is the case in described subspecies is not clear for all taxa. For birds, Phillimore and Owens (2006), based on a global analysis of avian subspecies, conclude that 36 % are phylogenetically distinct. A previous meta-analysis (Zink 2004) found only 3 % of the analysed subspecies to be phylogenetically distinct (based on mtDNA sequence data). However, this study was almost completely restricted to the Nearctic and Palaearctic and also considered mainly continental subspecies. Indeed, Phillimore and Owens (2006) found Nearctic/Palaearctic subspecies to show reduced levels of differentiation and continental subspecies to be less likely to be genetically distinct than island subspecies.

whose delimitation from the species level is fuzzy and bound to be arbitrary in many cases? Subspecies are mainly (although not exclusively) described under the Biological Species Concept, and many critics of this concept and/or adherents of other species concepts have raised exactly this kind of criticism. Wiley and Mayden (2000c, p. 199) hold that a large fraction of biodiversity is "subsumed into a black hole of terminal taxonomic neglect and ambiguity, better known as the subspecies category". Groves and Grubb (2011, p. 3) divide subspecies into "the Good, the Bad, and the Ugly". The good are diagnosable and hence, under their dPSC, "distinct species masquerading as mere subspecies—victims of the general feeling around the mid-twentieth century (and certainly under the influence of the BSC [= Biological Species Concept]) that taxa should be, if possible, relegated to the status of subspecies of the nearest species". The bad subspecies "are points along a cline, or are differentiated at very low frequency levels", making them interesting subject for research in, for example, population genetics, "but they have no taxonomic standing" (p. 4). The ugly subspecies are the rest. They can be differentiated from other subspecies but are not absolutely diagnosable. For these, Groves and Grubb use the subspecies category in their book and admit that there seems to be "some advantage in dignifying them with a trinomial, especially for conservation purposes, but as these ugly subspecies are arbitrary and unfalsifiable, one cannot insist on it" (p. 4).[41] Cracraft (1983, p. 171), another adherent of the dPSC, argues in a very similar vein:

> "*Subspecies cannot have ontological status as evolutionary units under a Phylogenetic Species Concept. While it therefore can be argued that this renders subspecies superfluous for systematic and evolutionary analysis, their continued use might be thought defensible under some circumstances. If one so chose, subspecies names could be applied to populations showing clinal variation, and subspecies boundaries could then be determined by sharp gradients in character variation. In this context, however, subspecies are merely descriptors of variation seen in sometimes subjectively chosen, nondiagnostic characters and do not represent taxa having independent ontological status. Because of this, I would recommend that subspecies names not be used. Only objective taxonomic entities should be classified.*"

The decisive point is whether there really is such a fundamental difference in objectivity between the species category and the subspecies category, whether this is a difference in kind and not only one in degree. Especially adherents of the dPSC would argue that the species category is objective while the subspecies is not, but in Chap. 6, I will argue that things might not be so unequivocal after all. And if there is only a difference in degree, subspecies advocates may argue that the subspecies, just like the superspecies, adds to our taxonomic arsenal to at least arrive at an approximation in our classifications of nature's fuzzy entities. Provided that

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[41] Granting subspecific names for differentiated populations in order to support conservation measures is the same kind of reasoning as the one that led Zachos et al. (2014) to describe *Cervus elaphus italicus* (see above). Note, however, that the Mesola deer meet the criteria of the dPSC and would have to be considered a "Good" subspecies in Groves and Grubb's view and thus a distinct species.

subspecies taxa denote real biological entities (however vague their boundaries) and thus give a name to a relevant portion of a species' diversity, they are indeed of potential value for conservation (see Chap. 7). However, since subspecies have often been described based upon very superficial phenotypic characters (scale counts, plumage colour, body size, etc.)—which had the advantage of being easy to study in, for example, museum collections—alternative concepts to the subspecies category have been suggested in a conservation biological framework. The most important of these concepts is the Evolutionarily Significant Unit (ESU). As stated in Chap. 4, this concept is sometimes also listed as a species concept, but originally (Ryder 1986) it was meant to provide a more objective infraspecific category for conservation purposes than the subspecies. An early and popular definition was given by Moritz (1994, p. 373, italics in the original): "*ESUs should be reciprocally monophyletic for mtDNA alleles and show significant divergence of allele frequencies at nuclear loci*". This definition has the advantage of being relatively easy to apply to real data. On the other hand, it neglects ecological data and adaptive significance of genetic variation (which were included in earlier definitions: Ryder 1986, Waples 1991). For this reason, Crandall et al. (2000), drawing on Templeton (1989, 1994), introduced the criteria of ecological and genetic exchangeability to delimit ESUs. "The central idea of ecological exchangeability is that individuals can be moved between populations and can occupy the same ecological niche. [... Ecologically exchangeable individuals exhibit] similar life history traits, ecological requirements, morphologies and demographic characteristics. Ecologically exchangeable individuals perform similar functions in each ecological community. [...] Individuals from different populations are genetically exchangeable if there is ample gene flow between populations. Unique alleles, low gene flow estimates ($N_m < 1$, where N_m is the effective number of migrants per generation) or phylogenetic divergence concordant with geographic barriers provide criteria for rejecting genetic exchangeability" (Crandall et al. 2000, p. 291f.). The authors then introduce an evaluation scheme for management actions based on evidence for ecological and genetic exchangeability in recent and historical times. For example, the two extremes of rejection of ecological and genetic exchangeability in both present and past and of confirmation of ecological and genetic exchangeability in both present and past lead to the populations being treated as long separated species and a single population, respectively. This approach is much more meaningful biologically than simple monophyly and significant divergence at mostly neutral genetic loci, but obviously the data needed to apply it are much more difficult to obtain. In any case, ESUs are not a taxonomic category with a specific name (unlike the subspecific trinominal) and will therefore only be relevant in an applied context (conservation and management)—which is, of course, the very aim with which the concept was introduced in the first place.

Chapter 6
Species Delimitation: Discrete Names in a Continuous World with Fuzzy Boundaries

"Nature proceeds little by little from things lifeless to animal life in such a way that it is impossible to determine the exact line of demarcation, nor on which side thereof an intermediate form should lie".
Aristotle, *Historia Animalium*, Book VIII, 588b, translation by D'Arcy Wentworth Thompson

"The problem is that despite the existence of a perfectly adequate concept and definition of species, most species are more like slime molds and sponges than like highly organized and tightly integrated multicellular organisms—at least in terms of their individuality. Not only can almost any part of a species give rise to a new lineage, but those new lineages also commonly reunite after separating. Consequently, there will be many cases in which it will be difficult to determine the precise number and boundaries of species—just as it is difficult to determine the precise number and boundaries of organisms in a fragmenting acrasialian pseudoplasmodium or a multioscular sponge. [...] The appropriate solution to the practical problem is simply to accept the inherent ambiguities of species boundaries".
Kevin de Queiroz (1999, p. 79f.)

The introductory quotation by Aristotle is not only a nice encapsulation of the idea of a great chain of being or *scala naturae*, but it also shows that, from the birth of Western science and philosophy, it has always been obvious that nature has fuzzy boundaries and that demarcation of similar entities is a difficult task. In Sect. 5.2 a potential theoretical solution to the species problem has been introduced: a hierarchical view that distinguishes between a true ontological or primary species concept and secondary operational species criteria. The ontological species concept (telling us what species taxa really are) is based on conceiving of species as population-level lineages or segments of such lineages as defined by the Evolutionary Species Concept or the General Lineage/Unified Species Concept. However, these concepts are non-operational, they just provide the framework within which species can and should be identified. Identification and delimitation of species taxa is what taxonomists are doing, and it is important that they are doing it within a consistent theoretical framework. The practice of species delimitation, however, is not guided by the lineage framework beyond the condition that species be lineages. Since the

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Tree of Life (and even more so the Web of Life in the prokaryotic world) is made up of lineages within lineages, the question whether there is an objective level of the species crucially depends on whether there is some (population) level within this fractal pattern that stands out. If that is not the case, then the species category, at least a single universal species category, is a myth: "What if there are theoretically important differences between the various segments of population lineages that we are identifying as species? Perhaps there are crucial differences between vertebrates, invertebrates, fungi and bacteria such that they should not all be regarded as forming the same kinds of species. What if, on our best theoretical understanding, there really do seem to be different kinds of species?" (Richards 2013, p. 60). If species taxa cannot be unified under the same kind of species category, then we would have to accept species category nominalism or at least species pluralism. Yet, even if we accept, for the time being, the hierarchical solution of the species problem as far as the theoretical side of the coin is concerned, species delimitation is a fuzzy business. I will argue that completely objective, non-arbitrary species delimitation is impossible and that the approach coming closest to this unattainable ideal is not feasible and biologically irrelevant, which leaves us with the insight that taxonomy, even at its best, is only going to be an approximation of the real natural pattern and, importantly, that species delimitation resulting in biologically meaningful entities can only be done in hindsight. In other words, it is theoretically impossible to arrive at a fully consistent, completely non-arbitrary and biologically meaningful classification of life. The main reason for this is that taxonomy is essentially binary—species or no (sub-/super-)species, one or two (sub-/super-) species, etc.—while the evolutionary process is continuous and will create inherently fuzzy boundaries. The practical side of the species problem, the actual delimitation of species, is what biologists are dealing with every day—either directly as taxonomists or indirectly as "users" of taxonomy when they count species, analyse and compare conspecific and interspecific populations, manage species, etc. It is therefore hardly surprising that species delimitation has received increasing attention, boosted undoubtedly by the methodological revolution in both genomics and bioinformatics. A Scopus search revealed that the number of published papers that had "species delimitation" in their title, abstract or keywords increased from 93 between 2001 and 2005 through 321 between 2006 and 2010 to 885 between 2011 and 2015 (see Fig. 1 in Camargo and Sites, 2013, for a similar finding). The available analytical approaches to species delimitation are diverse and comprise tree-based and non-tree-based methods. A more recent development is the implementation of coalescent theory, but there are also old ideas, such as the one regarding species as fields for recombination which originally goes back to Carson (1957) but has been revived by first Doyle (1995) and then more recently by Flot et al. (2010) and which delimits pools of alleles that recombine and co-occur in individuals. An overview and discussion of existing methods can be found in the following publications (and references therein): Sites and Marshall (2003, 2004), Knowles and Carstens (2007), Wiens (2007), Petit and Excoffier (2009), Birky et al. (2010), Ence and Carstens (2011), Fujita et al. (2012), Hey and Pinho (2012), Birky (2013), Camargo and Sites (2013), Carstens et al. (2013), Zhang et al. (2013).

There is even evidence that, across eukaryotic groups, a very simple correlation seems to exist between sexual compatibility and so-called compensatory base changes (CBC)[1] in the internal transcribed spacer 2 (ITS2) transcript secondary structure, such that the presence of even a single CBC seems to coincide very reliably (>90 %) with sexual incompatibility (Müller et al. 2007; Coleman 2009 and references therein). However, no matter if simple methods are based on genetic distances or morphological gaps or gene flow across hybrid zones or more complex methods such as tree-based coalescent models or cohesion tests, what all these approaches have in common is that they aim at consistently identifying lineages. What they do *not* do is objectively mark the level which is considered the species level: they make *grouping* (more) objective, but not *ranking*! This is why Sites and Marshall (2004, p. 220) conclude that "virtually all [methods of species delimitation] will require researchers to make qualitative judgments. For example, there is no objective criterion for how much morphological divergence is enough to delimit a species, what threshold frequency of intermediates is needed to delimit species by genotypic clusters [. . .], what proportion of unlinked loci are needed to delimit coalescent species [. . .], or what frequency cutoff most appropriately indicates that no significant gene flow is occurring between populations". There simply is no silver bullet for species delimitation. The available species delimitation methods become ever more sophisticated, but they only help us identify *lineages*; none of them can answer the question of where the line of the *species* lineage should be drawn. They will always entail a decision on some kind of cut-off criterion. But an arbitrary cut-off criterion that can be *measured or tested for* objectively is *not* the same as an objective delimitation criterion! The sooner we recognize that some arbitrariness is naturally inherent in species delimitation, the earlier we can focus on biological phenomena, not names. The grey area during lineage divergence is a field of exciting evolutionary and ecological phenomena and for research that should not be spoiled by endless and ultimately futile debates about how to make species delimitation absolutely objective. I will not discuss concrete species delimitation algorithms here but rather focus on the more general aspects and difficulties surrounding delimitation in a world of fuzzy boundaries.

6.1 The General Problem: Discrete Names in a Continuous World

Let us begin with a little thought experiment. If only elephants, mosquitoes and tulips existed, would there be a delimitation problem? Certainly not among the three groups, only (if at all) within them. Delimitation thus only becomes problematic when zooming in on the Tree of Life, when considering entities that have not

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[1] CBCs occur in paired regions of RNA transcripts when both nucleotides at a paired site mutate such that the complementary pairing is maintained (e.g. a mutation from G-C to A-U).

been separated very long and have not accumulated such an amount of distinctness that their identity as a distinct entity is obvious. *Homo sapiens*, for example, has not even been described officially (Linnaeus's famous "description" was *nosce te ipsum* or "know thyself"), yet our status as a distinct species among *extant* organisms is never questioned (it becomes much less clear when including extinct hominids).[2] It has been repeatedly argued in this book that because of the fractal nature of the Tree of Life—its being composed of lineages within lineages—the identification of a distinct level of lineages, the species category or rank, is a contentious issue. Names and language, and therefore also taxonomy, are discrete, while evolution is continuous. This discrepancy is real and cannot be bridged, and this is what ultimately makes species delimitation so difficult. The importance of this insight can hardly be overestimated because it makes at least parts of the species debate inherently futile. There are, however, other problems with respect to continuousness, not just the fact that evolution is continuous. In fact, many biological concepts, and certainly many that are important in the species debate, are a matter of degree and in that sense also continuous. Reproductive isolation, for example, is a case in point: "Simply saying that species are reproductively isolated fails to capture the point that reproductive isolation is a matter of degree" (Ghiselin 1997, p. 100; see also Lee 2003). Horses and donkeys sometimes, although rarely, produce fertile offspring—does that make them a single species, although the two lineages clearly evolve independently of one another? The Hennigian Species Concept with its emphasis on absolute reproductive isolation seems to insinuate this. And how about cases where one sex is always sterile? Is it biologically meaningful to lump everything into the same species that once in a blue moon produces fertile hybrids and thus introduces single alleles into each other's gene pool? There is a continuum from complete isolation via occasional introgression and regular introgression confined to small fractions of the genome to isolated "speciation islands" in the genome (see the crow example in Sect. 5.4), and finally a completely homogeneous panmictic population. It is becoming increasingly clear that what is considered to be the species boundaries, those "phenotypes/genes/genome regions that remain differentiated in the face of potential hybridization and introgression", are "semipermeable, with permeability (gene exchange) being a function of genome region" (Harrison and Larson 2014, p. 795; see also Walsh et al. 2016).

Even more important is that not even allopatry can be unambiguously defined. Under a lineage-based species ontology, species are separately evolving

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[2] Humans are an interesting example. It has independently been pointed out by several authors that Phylogenetic Species Concepts, and in particular the dPSC, would result in the splitting of *Homo sapiens* into several species (Willmann and Meier 2000; Ghiselin 2001; Zachos and Lovari 2013). On the other hand, there is even evidence that palaeoanthropological data are in line with a single anagenetic lineage for *Homo* in its totality (Van Arsdale and Wolpoff 2013; Wolpoff, personal communication). This stands in clear contrast to the 10+ species of *Homo* that have so far been described. The scientific and medial attention that comes with the description of a new fossil human species may contribute to researchers being more prone to splitting in this case (White 2014).

population-level lineages. But when exactly are two lineages separately evolving? This is a difficult question. The only seemingly objective solution, and one that has indeed been pointed out, is to assign species status to the only population level that can be (allegedly) delimited non-arbitrarily, i.e. the lowest. This means equating the species category with allopatric populations because allopatric populations are by definition separate lineages, regardless of whether or not they are diagnosable, monophyletic, ecologically different, reproductively isolated, etc. Objectivity is only attainable at the cost of accepting as species all spatially separate groups of organisms: "If species are individuals, i.e. populational systems, it follows that geographically isolated populations are different species" (Mahner 1993, p. 110). As a consequence, it has been suggested to have not only one but two classification systems—one that serves as a convenient information storage system but disregards truly objective ranking criteria and one that is based on strict scientific and logical consistency (e.g., Kunz 2012, p. 44). In other words: one would deliberately have a classification of T species and one of (hypothesized) E species. Kunz (2012) advocates the notion of species as gene flow communities, and therefore accepting any kind of gene flow disruption as the ultimate arbiter (whether intrinsic or extrinsic, temporary or permanent) is the only non-arbitrary way of delimiting species. After all, gene pools in allopatry become abstract entities (Stamos 2003, p. 196). Such a logically consistent system, however, is impossible to realize. It would have to accept every little allopatric offshoot of a larger population as a distinct species because the connection between the two is interrupted, even if this is only temporarily the case. For example, every little propagule of every fly or mosquito species that is dispersed in aircraft across the world and survives (and reproduces?) would have to be considered a distinct species. The same holds for every population of goats or tortoises on Mediterranean islands and every closed breeding group in captivity. If you add to this the demand of the Hennigian Convention that upon species splitting the ancestral species goes extinct, you will have to rename the original fly or mosquito species every single time a propagule gets dispersed—probably hundreds of times every day! It is very obvious that any such attempt could at best mitigate the inconsistencies of our present system - a truly objective system based on allopatric populations is unattainable in practice, and if it were, it would serve no purpose. This is what I meant earlier when I said that the (biological) baby is thrown out with the bathwater or that biological relevance is sacrificed on the altar of logical consistency. But there is a deeper lesson behind this example: allopatry is a matter of degree, too. How far away from the mother population must organisms venture to count as "allo"-patric? One kilometre or two? Twice the usual dispersal distance or only 1.5 times? And how many individuals constitute an allopatric population? Is a single pair enough or even a pregnant female? A single individual in asexual organisms? And how often must the allopatric group reproduce, for one generation or two or 31? What is seemingly an inconvenient but at least objective cut-off criterion turns out to be very inconvenient indeed, but unfortunately not so objective after all.[3] This is by no means a new insight. Remember, for example, Poulton's judgment quoted in Sect. 2.4: "transitions are infinite in their variety; while the subjective element is obviously dominant in the selection of gaps just wide enough to constitute interspecific breaks, just narrow enough to fuse the species separated by some other writer, dominant also in the choice of the specific characters themselves" (Poulton 1904, quoted from Wilkins 2009b, p. 114). The conclusion that some draw from this is species category nominalism (see Sect. 3.6): "Species are equivalent by designation, only not in terms of their state of evolutionary, genetic or ecological differentiation or divergence" (Heywood 1998, p. 211). But because a truly non-arbitrary classification is impossible one might as well go on with a flawed but practical one (but be aware of it!): "the species must continue to be defined pragmatically by practising taxonomists in the way that most effectively divides the group of organisms in question into units which it is useful to recognize and name, bearing in mind the needs of the various user groups. Comparisons across classes of organisms in terms of species must be treated as no more than general indications of amounts of biodiversity, not as precise statistics" (ibidem). The last part of this quotation encapsulates what is so important about having an objectively real species rank: comparative analyses based on species taxa. The ramifications of this will be discussed in Chap. 7.

It is worth noting that while messy situations are expected under an evolutionary paradigm—in fact, the lack of messy situations would be a serious blow to the theory of evolution, as has often been stated (e.g. Stamos 2003, p. 332[4])—most pairwise comparisons between any two populations of organisms on earth are unequivocal as the introductory example of the elephant, mosquito and tulip has shown. Similarly, nobody doubts the distinct species status of newly discovered organisms that have no close living relatives,[5] such as the coelacanth, the okapi or *Symbion pandora*. It is only among taxa going back to a common ancestor in the recent past that things become fuzzy (the grey area in the speciation process in Fig. 5.2). However, this "excuse" only holds with respect to whether there are one or two lineages. The problem of ranking these lineages remains.

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[3] Kunz (2012, p. 133) correctly argues that a descent community only has connection, but not delimitation, and therefore boundaries must be added through convention. He views species as gene flow communities as the solution, because gene flow communities show both connection and delimitation. Again he is right. However, he is wrong when he believes that this is a clear-cut solution because, as shown, even if all allopatric groups were considered distinct species, boundaries would still be vague due to the continuous nature of allopatry itself.

[4] Stamos suggests the term "messyspecies" for the grey area along the sundering process of lineages.

[5] Of course, every population or species has a clos*est* relative, its sister taxon. This follows from the unique origin of life on earth. What is meant here is that the closest living relative, i.e. the *extant* sister taxon, and the newly discovered organism go back to a common ancestor that lived long enough ago for the two daughter taxa to have diverged beyond doubt as to their distinct species status.

One almost universal consensus with respect to ranking, suggestions regarding two separate classifications (see above) notwithstanding, is to assign species status only to non-ephemeral entities to avoid the problem of having to name every short-lived allopatric population: "all concepts avoid naming formal species taxa where they might be ephemeral or temporary (e.g., small geographically isolated populations), even when they otherwise fit the criteria of the concept. Some judgment of significance is involved" (Mishler and Theriot 2000b, p. 121). Mishler and Theriot (ibidem, p. 132) compare this judgment of significance with respect to species taxa with higher monophyla: not all of these must be named, just the ones we deem worthy of it because we need this for our communication. "It is alright [...] to be subjective if by that we mean naming only those lineages (at whatever level) we have reason to talk about". It should be remembered here that Mishler and Theriot do not think that a distinct species level exists, but that the species rank is as arbitrary as that of higher taxa and that only nested monophyletic groups exist. This makes it easier for them to allow for subjective judgment, but in principle, the question whether or not this is necessary is independent of their views of the species rank. The avoidance of naming ephemeral entities is the reason why many authors agree that species delimitation can only be meaningfully achieved *in hindsight*, i.e. after lineages have been separated for enough time to evaluate whether the split is or is going to be permanent. This is why Kornet, in her internodal species concept, insists on permanent splits (strictly speaking, only extinction is conclusive evidence of a split being permanent), and this is also the rationale behind the second half of the Evolutionary Species Concept ("own evolutionary tendencies and historical fate"). Stamos's claim that this is teleological "backwards causation" has already been rejected in Chap. 4 (see footnote 11).

Sober (1984) and O'Hara (1993) explicitly defend the retrospective approach in species delimitation. O'Hara (1993) specifically analyzes the Evolutionary, Biological and Phylogenetic (diagnosability) Species Concepts, but in principle what he says applies to any species concept: that they "depend upon prospective narration: upon notions of fate, temporariness, and permanence", and he considers "Wiley's explicit recognition of future dependence, under the name of 'historical fate', to be particularly insightful" (p. 242). Sober (1984, p. 339) argues in a very similar fashion: "species individuation is retrospective [...] The founders were founders of a new species precisely because of what happened later, and not in virtue of anything special about them. In the same way, an offspring may be as different as you wish from its parents. Whether it falls into a new species depends on what happens later". In a footnote to this paragraph, Sober cites an old TV programme where someone read a newspaper whose headline reads "World War I breaks out!" Of course, upon its outbreak World War I was not yet World War I (that it only became when there was also a World War II), and Sober writes that species delimitation is settled in the same way. That lineage divergence is, for quite some time, reversible has been shown by incidents of so-called reverse speciation where mate-choice-induced reproductive isolation broke down again (Seehausen et al. 1997; Seehausen 2006; Maan et al. 2010, Vonlanthen et al. 2012, Grant and Grant 2014, Kleindorfer et al. 2014; see Sect. 1.4). Upon the strict view of species being irreversibly diverged lineages, speciation would not have been complete in these cases and the term "reverse speciation" would be flawed, but this is only a terminological issue. Also, accepting every permanent split as a speciation event and thus the daughter lineages as species has the bizarre and unintended (although logically consistent) consequence that an allopatric propagule that dies out after a single generation would have to be assigned species status, and this "is not what is meant by a species in most theories of speciation" (Ghiselin 1997, p. 115). The decision, ultimately at least partly arbitrary, which level of distinctness one ranks as specific will therefore have to be based not only on genealogy but on something else as well. The obvious candidate—and the one that is being used by most—is some measure of similarity (see Sect. 6.4).

6.2 The Tokogeny/Phylogeny Divide: Saviour of the Species Rank?

The question if we can delimit species completely non-arbitrarily has been answered in the negative in the preceding chapter. But that does not mean that species delimitation must be completely arbitrary either. However, for the species rank to be biologically meaningful, it has to be different from all other ranks that lineages can have in the Tree of Life. That there is such a unique level is denied by some whose position is called species category nominalism (see Sect. 3.6). Remember, for example, Mishler (1999, p. 309): "we have no and are unlikely to have any criterion for distinguishing species from other ranks in the Linnean hierarchy, which is not to say that particular species taxa are unreal. They are real, but only in the sense that taxa at all levels are real. Species are not special". Similarly, Mishler and Theriot (2000a, p. 48) write that "there is no species problem per se in systematics. Rather, there is a taxon problem. Once one has decided what taxon names are to represent in general, then species taxa should be the same kind of things, just the least inclusive". And indeed, it is not easy to find a criterion by which the species level could be uniquely described, although "[b]iodiversity does appear to be clustered around species, even if un-sharply so, and species themselves recognize these organized clusters" (Rieppel 2007, p. 378). Probably the only qualitative break within the fractal pattern of the Tree of Life is the level where reticulate relationships among organisms *within* lineages dissolve into the hierarchical relationships *between* lineages. This is the famous tokogeny/phylogeny divide (Hennig 1966, especially his Fig. 6). It is the sundering of two populations within which there is horizontal reticulation through reproduction but between which there is not. There is only one such level in the Tree of Life, and it is at the level of populations, which makes it the ideal candidate for an objective demarcation criterion for the species category. Above this level, which is itself phylogenetically indivisible, there is the realm of interspecific relationships as analysed by phylogenetic analyses aiming at finding monophyletic groups; below this level is the realm of intraspecific population biology.[6] Accordingly, this distinction is viewed by many as the solution to the question about the species rank. However, there are some serious problems with this view.

First of all, asexual organisms do not have tokogenetic relationships if by this reticulation through sexual reproduction is meant.[7] In asexuals, hierarchical relationships go down to the level of the individual organisms. In other words: there is no tokogeny/phylogeny divide in asexuals. This leads us back to the question if "species" can refer to the same thing in sexuals and asexuals or whether asexuals form something else altogether ("agamotaxa" or "agamospecies", see Sect. 5.1). Perhaps we have to accept that a unique species level only exists in sexually reproducing organisms. But then, reproduction is a continuum with exclusively sexual and asexual reproduction as its extremes but many organisms in between. It may thus not even be clear in all cases whether the tokogeny/phylogeny divide is applicable or not. A second problem is that what the tokogeny/phylogeny divide really denotes is the point where one reproductive community splits into two and that is first and foremost the case when a formerly connected population splits into two allopatric populations. That is, the real level of the tokogeny/phylogeny divide sensu stricto is *below* what is usually recognized as the species level. To raise it to the level where only non-ephemeral and (what we consider) biologically meaningful entities would be assigned species status, we have to refrain from classifying recently sundered lineages but confine ourselves to those which, in hindsight (!), have proved to be not only temporarily separate entities but lineages with a unique "historical fate". That is, the tokogeny/phylogeny divide alone is not enough—it must be complemented by some kind of threshold to avoid assigning species status to every allopatric population. Another problem is that gene flow occurs at higher levels, too. Reticulation, according to Mishler and Theriot (2000a) occurs throughout the Tree of Life, and Vrana and Wheeler (1992, p. 68) argue that Hennig's figure showing the divide "presumes that some inexplicable process at the 'Species' level renders an entirely clean break between reticulation and divergence, that this break is obvious, and the process is constant across all organisms. In other words, this figure rather than an empirical fact, *is an unfounded process statement*". That this break is anything but "entirely clean" has, I think, become sufficiently clear so far. In fact, rather than a break or line, it is an area with, once again, fuzzy boundaries, and reticulation through hybridization can occur long after the splitting of the lineages that we usually call species. The more species groups are analysed genetically and the more sophisticated our genetic methodologies become, the more it becomes obvious that interspecific introgression is rampant, that reproductive

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[6] These two levels, being represented by phylogenetics and population genetics, respectively, for a long time developed independently and in parallel but were ultimately united by phylogeography and the insight that stochastic processes within populations had deeper implications for phylogenetics (gene tree/species tree discordances) (see Sect. 5.6.1).

[7] Mishler and Theriot (2000b) argue that tokogeny is not the same as reticulation but that it is parent–offspring relationships in both sexuals and asexuals. This is, as far as I know, an unusual interpretation, and in any case, they are of course aware of the lack of reticulation in asexuals.

isolation can remain incomplete for millions of years and that large fractions of the genome of different taxa may be compatible, rather than represent coadapted genetic systems whose disruption through hybridization leads to fitness reduction (outbreeding depression due to Dobzhansky–Muller incompatibilities) (Mallet 2005; Mallet et al. 2007, 2016; Harrison and Larson 2014; Abbott et al. 2016; Crossman et al. 2016; Payseur and Rieseberg 2016; Walsh et al. 2016; Wen et al. 2016). Mallet (2005) estimated that at least 25 % of plant species and 10 % of animal species are subject to interspecific hybridization and potential introgression. In some cases hybridization may lead to the fixation of alleles in a different species due to a selective advantage. A well-known example for this is the complete ("mitochondrial capture") or near-complete fixation in Iberian hare species (particularly brown hares *Lepus europaeus*, but also, to a lesser degree, *L. granatensis* and *L. castroviejoi*) of mitochondrial DNA of mountain hares (*L. timidus*)—which have been absent from the region for several thousand years! The widespread occurrence of mountain hare mtDNA might be the result of a selective sweep because mitochondrial DNA is involved in heat production, and mountain hare alleles could be advantageous in areas of high elevations (such as the Pyrenees where the level of introgression is particularly high) (see Alves et al. 2008 and references therein).

To sum this up, there are a lot of drawbacks with the tokogeny/phylogeny divide, but it may be all we have to defend the view that there really is a unique species level, at least for completely or predominantly sexual organisms. And the fact that this level is fuzzy and slippery, so that we cannot exactly give its boundaries, does not mean that it does not exist. What it does mean, though, is that we should not take for granted that what bears the name species is necessarily all of one and the same kind!

6.3 "Chronospecies", Ring Species and a Delimitation Analogy with Languages

The concept of chronospecies for a segment along a single unbranched lineage that is assigned species rank for its showing some diagnostic feature is frequently used in palaeontology. It may be convenient to give different names to organisms with different traits because it facilitates communication, but from a theoretical point of view, the cutting up of a continuous lineage is hard to defend. Species must be delimited in space and time. It has been shown in previous chapters that spatial delimitation (the synchronic delimitation of species boundaries) is very difficult and that a completely non-arbitrary delimitation is not possible—exactly how inclusive a species may or must be, i.e. where exactly the level of the species rank is with regard to allopatric populations, necessarily requires some kind of ranking criterion that cannot *only* be based on genealogy. In the temporal dimension, this is much easier from a theoretical point of view: single continuous unbranched lineages cannot be subdivided objectively and don't have to be. They can and should be simply classified as a single species.[8] The essential difference between the spatial and the temporal dimension in this regard is that delimitation in space is about which of *different real* levels of lineages stands out as the species level (if indeed this level exists), while the temporal approach of cutting up continuous unbranched lineages does not produce real units at all, at least not if a real unit has to be a historical individual in this context. Therefore, whatever units are delimited when accepting "phyletic speciation", they are ontologically very different from those delimited by cladogenetic evolution. Of course, biologists and palaeontologists are free to subdivide lineages into morphs, chronospecies, etc. and attach names to them to facilitate communication, but it should be made clear that these are fundamentally different "species" than the ones we try to identify as real historical entities. For example, they should not get normal binominals but should be marked in some way.

That it may be very difficult or even impossible to decide whether a sequence of fossils belongs to a single continuous or several lineages is a different, practical matter and of no relevance to the theoretical invalidity of chronospecies. Accepting that there is no non-arbitrary way of cutting up a single lineage, Gould (2002, p. 776) cynically remarked that this topic "generated a large, tedious, and fruitless literature, primarily because the issue always remained available, unresolved and therefore ripe for yet another go-round whenever a paleontologist needed to deliver a general address and couldn't think of anything else to say". Nevertheless, there are proponents of chronospecies in both science and philosophy. The scientific attempts at justifying chronospecies—equating speciation with the fixation of a formerly polymorphic trait, regardless of whether this is accompanied by lineage sundering or not—have been presented in Sect. 5.6.2 when the diagnosability version of the Phylogenetic Species Concept *sensu* Wheeler and Platnick was discussed. The philosophical defence of dividing unbranched lineages into different species is put forward by David Stamos, and he combines this with an analogy with languages (see below). The analogy of languages and species has a long history, and it was prominent also in Darwin, but the comparison of languages and species is usually made in the context of evolving entities or systems, although early on August Schleicher pointed out that there is also a delimitation analogy (see Sect. 1.6). This latter analogy pertains to the distinction between languages and dialects in linguistics and the distinction of the specific and the intraspecific level (Darwin's species vs varieties) in biology. In both cases, boundaries are fuzzy, and there is a continuum from well-differentiated languages (sometimes called "languages by separation") and species at one end of the spectrum to completely homogeneous entities at the other, with all kinds of transitional stages in between. The linguistic analogue of interfertility is mutual intelligibility: the "criterion for distinguishing

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[8] Theoretical problems actually only occur with branching and the question whether every branching event should result in one or even two (Hennigian Convention) new species (see Sect. 5.5). As long as there is no branching, however, there are no such problems, and regarding a single continuous lineage as numerically the same species throughout its existence is an objective way of classification and the only objective way in line with species being historical individuals.

'dialects' from 'languages' is taken, in principle, to be that of mutual intelligibility" (Matthews 2014, p. 104; see also Ghiselin 1997, p. 140). Matthews gives Dutch and English as an example for two different languages and Dutch and Flemish as two dialects of the same language, and he also makes it clear that the distinction between languages and dialects is "a matter of degree" (ibidem). Dutch and German are closer to one another than either is to English, but clearly they are two different languages. I am a native speaker of German, and I cannot understand Dutch. Or can I? That depends upon the level of complexity. Simple sentences in party small talk or in a travel guide ("turn right at the big tree") may not be a problem, but I cannot follow a more complex conversation in Dutch. Speakers of Spanish and Italian can communicate rather well with one another up to a certain level of complexity, but nonetheless both languages, just like Dutch and German, have distinct grammars, separate literary traditions and are on independent linguistic trajectories. Just like separately evolving population lineages under the Evolutionary and General Lineage Species Concepts, they can be considered different languages, yet the boundaries are just as fuzzy. Mutual intelligibility is just as much a continuum as is interfertility and basically every other delimitation criterion for species. In the case of languages, things get further complicated by the fact that there is spoken and written language, and intelligibility may be very different for the two. I understand much more Dutch when I read it than when I hear it, and the same holds for speakers or readers of, for example, Danish and Norwegian. In some cases (e.g. Cantonese and Mandarin Chinese), mutual intelligibility is near perfect for the written language, but practically absent in speaking (although admittedly, in this case the written language is based on logograms rather than on phonograms).

But what about the temporal dimension? There is a fundamental difference here between organisms and languages. Extinct and extant organisms cannot interbreed, nor can we definitively answer the question if they could, but in languages this is different because we have written sources. It is therefore clear that a native speaker of English today cannot understand Old English. Still, they are (in all likelihood) both part of a single unbranched lineage. We find ourselves in the dilemma of either accepting "linguistic chronospecies" or accepting that speakers of numerically the same language do not understand each other (through time). Ghiselin (1997, p. 141) is very clear on this: "although it [English] has undergone much dialectical diversification, English has never undergone the analogue of speciation. The language of Beowulf, the Canterbury Tales, Hamlet and Huckleberry Finn has changed a great deal without ceasing to be one and the same individual language". This may be counterintuitive and contrary to the way we normally use the word language but that only shows that we emphasize one aspect of language: its function as a means of communication. We are rarely occupied with linguistic evolution through time. Sometimes these two notions clash, and the scientific treatment of languages, which are historical individuals just like species, has to give genealogy priority over functionality, i.e. history trumps mutual intelligibility. The fact that loanwords, which are the analogues of interspecific gene flow, do not undermine the integrity of either of the two languages involved, further adds to the validity of assigning language rank, just like species rank, when and only when one is dealing with entities that are on separate and diverging trajectories. All the German loanwords in the English language (leitmotif, angst, kindergarten, blitzkrieg, etc.) and even all the French words incorporated into English since 1066 have not changed the fact that English is fundamentally independent of these two languages. For both word and gene flow alike "[w]hat matters is not that all gene [/word] flow be cut off, but that it be cut off to a sufficient degree that the species [/languages] can continue to diverge instead of fusing back together into a single populational [/linguistic] individual" (Ghiselin 1997, p. 96).

David Stamos (2003, p. 263) strongly objects to this view and argues based on an analogy with languages: "the absurdity of the view that a species might retain its numerical identity [i.e. stays one and the same] through infinite evolution becomes strikingly apparent when we apply it to the closest analogue to species, namely languages. Suppose a language undergoes 'infinite evolution' without branching. Although it is historically true that linguists have been interested in the 'phylogeny' of languages earlier than have biologists in the phylogeny of species, surely few if any outside of cladism and its cognates would ever want to defend a *cladistic language concept*, in other words the view that a language which undergoes 'infinite evolution' without branching is numerically the same language from start to finish". He argues with the "crystal-clear criterion" (ibidem) of mutual intelligibility and considers the fact that Ghiselin thinks Old English and Modern English as being the same language as a concession to consistency because he argues against splitting up lineages into chronospecies. He further distinguishes languages from "language lineages" and holds that what he calls the cladistic language concept is a concept of the latter rather than the former—analogous to Bock's (2004) distinction between species and phyletic lineages (see Sect. 1.4, Stamos quotes Bock in this context). This does not solve the problem, though. It only gives two different names to the synchronic and the diachronic dimensions of one and the same historical individual. If an extinct language is resurrected (like Hebrew), it is the same language according to Stamos because extinction is not necessarily forever—neither for languages nor for species. That this argument is not conclusive (for Stamos's cause) has been shown in Sect. 3.2 where the resurrection (e.g. through cloning) of extinct species was discussed. Just as the cloned dodo is an extension of the original gene pool (either directly through DNA from a subfossil specimen or indirectly through copying that exact DNA sequence in the laboratory), Modern Hebrew is based on written sources of the original old language. In both cases the information on which the original and the resurrected entities are based is *homologous*. A completely independently evolved identical dodo or Hebrew language would have to be considered a distinct species or language, but that is a purely academic issue. In the case of hybridization between the two dodo populations, they would then merge into a single hybridogenic species. The reason why Stamos readily accepts linguistic and biological speciation along an unbranched lineage is that he considers the synchronic dimension of species (and languages) as superior (see Sects. 1.4, 3.2, 3.5 and Stamos's biosimilarity species concept in Chap. 4). This, however, necessarily destroys the integrity of historical entities. Stamos is of course free to define species as phenotypic similarity complexes, but many (if not most) biologists will refuse to follow him in this and accept the disruption of the continuous historical entities that species are. With respect to languages, one might add that Old English and Modern English are not the same language based on the criterion of mutual intelligibility, but that criterion is not the only one as far as languages as historical entities are concerned, although it is by far more important than the interbreeding or interfertility criterion for species. For the latter, there are many secondary species identification criteria, and failure in meeting one of them does not necessarily entail that two entities are conspecific. Accepting the priority of species being historical entities over their being groups showing similarity—and this priority should be clear from the fact that similarity is a direct consequence of historical connections (common descent)—may lead to uncomfortable conclusions. Darwin's famous bear that might evolve into a creature "as monstrous as a whale" (Darwin 1859, p. 184) would be, if that evolutionary process were to be only anagenetic (i.e. without splitting), numerically one and the same species throughout its entire existence. That is counterintuitive, perhaps even ridiculously so, but first of all, it is very easy to sketch ridiculous situations for all ways of species delimitation; second, it is only counterintuitive because we are used to thinking in categories based on similarity (see Sect. 3.4) and to observing species mainly in one time horizon; and last, it is more than likely that such a scenario is, if at all, a very, very unusual exception. On the other hand, if we give up the priority of history, taxonomy will lose its single most important objective basis on which it can claim to be a rigorous scientific discipline. Ereshefsky (2010b, p. 676) was right when he stated that capturing similarity "is not the aim of biological taxonomy. Its aim is to capture history".

Interestingly, there is also a linguistic analogue of ring species: the dialect continuum, which is defined as a "range of dialects distributed geographically across a territory, such that adjacent varieties are mutually intelligible but those at the extremes are not" (Matthews 2014, p. 105[9]). Ring species, for comparison, are usually defined as a series of adjacent populations that curves round on itself in such a way that the populations at the extremes overlap but are unable to interbreed successfully while at the same time being connected by gene flow via the populations between them. The geographical proximity of the extremes is essential to the ring species definition, whereas for the dialect continuum, this is not necessary because speakers of the two extreme dialects can talk to each other even without direct contact of their dialect distribution ranges. Ring species have gained a lot of attention because of the taxonomic dilemma that two reproductively isolated sympatric or parapatric populations experience gene flow via intermediate populations—are they one or two species then? Yet, by now we are well familiar with the existence of taxonomic grey areas, and besides ring species are not so special after all, but "exceptional only with respect to the fact that distant individuals of a species encounter each other under natural conditions. Otherwise, a ring

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[9] The extreme and mutually unintelligible dialects in Matthews's example are those spoken a century ago in rural Devon and Glasgow.

species is nothing other than the normal phenomenon of isolation by distance" (Kunz 2012, 165). Isolation by distance means that there is a correlation between geographic and evolutionary (genetic) distance, because gene flow is usually negatively correlated with distance. Ring species are particularly well known in ornithology, although one of the most widely known textbook examples, the herring gull complex (*Larus argentatus* and related taxa), does not seem to fulfil the above definition (Liebers et al. 2004). There are better candidates, like greenish warblers (*Phylloscopus trochiloides*) and Indo-Malayan bulbuls (*Alophoixus* spp.) (Irwin et al. 2001; Martens and Päckert 2007; Martins et al. 2013; Fuchs et al. 2015; Pereira and Wake 2015), and these examples are fascinating cases of the study of evolutionary differentiation and divergence, but their impact on the evaluation of species concepts and the problem of species delimitation has probably been exaggerated—they are, quite simply, just another example of fuzzy boundaries.

6.4 Similarity and Attempts at Standardizing the Assignment of Species Status

> "*The one thing that all real species share, along with all of our categories that we equate with real species, is similarity among their member organisms.*" Jody Hey (2001a, p. 173)

If species are ontologically, above all else, conceived of as historical entities, then similarity cannot and indeed must not be a definiens of species. Nevertheless, similarity is important when it comes to the issue of species, despite its having been maligned as typological and essentialist. Even the vilified overall similarity does play a role. However difficult the quantification of overall similarity may be, Stamos (2003, p. 342) correctly points out that probably everyone would agree that two zebras have a higher degree of overall similarity than a zebra and a cockroach, and this is the reason why in the thought experiment in Sect. 6.1, there is no species problem when comparing elephants, mosquitos and tulips. That overall similarity may be difficult or even impossible to be measured objectively because one can never analyse all characters does not matter here—in the case of zebras and cockroaches or elephants, mosquitos and tulips, measurements are unnecessary.

In the last chapter, it was argued that vertical species delimitation is theoretically simple as long as there is no branching. Single unbranched lineages must be classified as numerically the same species through time. Even if in practice it may often be impossible to decide whether there was cladogenesis or not, in theory the situation is, I think, unequivocal. But what about the extension of species in a cross section through the Tree of Life? Which population-level lineages should be subsumed under the same species and which should be classified as different species? In other words: what should be lumped and what should be split? Cases in which what is considered a single species turns out to be comprised of different and not closely related lineages are easy to deal with once (and if) they are uncovered. The “species” would then be a polyphyletic group whose status was wrongly inferred based on similarity due to homoplasy or convergence. In that case, there are either two distinct species or one of the two independent lineages is part of another already known species. This is equivalent to polyphyletic taxa at higher levels in the Tree of Life that, once recognized, must be split. For example, the “Insectivora” of older mammalian classifications are now known to be polyphyletic, the two monophyletic but not closely related subgroups being the Lipotyphla (or Eulipotyphla: hedgehogs, shrews, moles and others), which are part of the more inclusive taxon Laurasiatheria, and the Afrosoricida (tenrecs, golden moles), which belong to the Afrotheria. The two lineages have been separate for tens of millions of years. Analogous cases of polyphyletic species are found, for example, in golden jackals and European vipers. The golden jackal (*Canis aureus*) was considered to occur from Southeastern Europe through Arabia to Southern and Southeast Asia, but also in Northern and Eastern Africa. The African populations, however, have recently been found to be an unrelated lineage within the Canidae, more closely related with wolves and coyotes than with golden jackals (Koepfli et al. 2015), and are now considered a distinct species, the African golden wolf (*Canis anthus*) that shows surprising morphological convergence with the golden jackal. In a similar herpetological case, it has recently been found that a population of vipers in the Italian Alps is not part of the common adder (*Vipera berus*) but in fact phylogenetically closer to species in the Caucasus and has consequently been described as a new species (*Vipera walser*, Ghielmi et al. 2016). It is the cases without polyphyly that are tricky because then one ultimately has to draw the line somewhere within a continuum of lineages within lineages (Fig. 6.1). Unfortunately, here there is no such golden yardstick as in the vertical dimension of a single unbranched lineage.[10] The problem of delimitation shown in Fig. 6.1 has a parallel when it comes to naming clades (see also Mishler and Theriot 2000a, p. 47f.). The name Mammalia is attached to the extant clade comprising monotremes, marsupials and placental mammals. Why is it not attached to the clade comprising these three groups and their immediate extinct sister taxon? Or the next sister taxon as well? Or why not only to marsupials and placentals, arguing that the monotremes should not be included because of their being oviparous? Which groups are monophyletic is a clear-cut issue (provided phylogenetic reconstructions are correct), but how inclusive the clade should be that bears a particular name is not. There is some arbitrariness involved, and one has to keep this in mind when asking for the most speciose taxon (insects perhaps, but why not insects plus their sister group!?) or for the age of Mammalia or any other taxon. The nested hierarchical structure of the

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[10] And it is worth remembering that the golden yardstick shines much less brightly as soon as branching comes into play (does the stem species survive, and if so, which of the two is it?)!

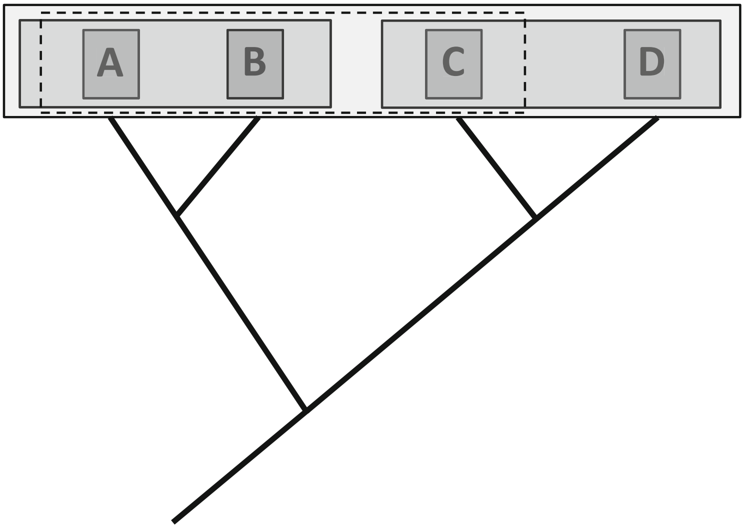

Fig. 6.1 The problem of horizontal species delimitation. Let us suppose A through D are allopatric populations and thus, at least temporarily, separate population-level lineages. Should one assign distinct species status to each of the four, to the next higher level (two species: A/B and C/D), only to the highest level (a single species A/B/C/D) or a combination of two levels (three species, e.g. A, B and C/D)? Because of the nested structure of the Tree of Life ("lineages within lineages") that is shown here with differently shaded boxes, genealogy alone does not yield a sufficient delimitation criterion, only a necessary condition (species must be population-level lineages). Ultimately, a cut-off criterion for the species level must be introduced, and this criterion will include some measure of similarity. The dashed line circumscribing a species A/B/C is supposed to highlight that species need not be monophyletic. Monophyly is only applicable to non-reticulating systems above the species level (see Sect. 5.6.1)

Tree of Life makes many such questions doubtful or even meaningless.[11] The fact that a similar reasoning might also apply to species inasmuch as their horizontal inclusiveness is concerned (see Fig. 6.1) is a worrying thought, but an important one (see Chap. 7).

In line with the view that there is no *ontological* difference between synchronic and diachronic species, and since similarity is not an *ontologically* relevant criterion for species, one could, however, argue that from an *operational* point of view, synchronic and diachronic species differ with respect to similarity and that similarity may be used in horizontal species delimitation. Splitting up a single unbranched lineage through time and having a cut-off criterion for horizontally delimiting a level are two fundamentally different things. Because there is no (onto-)logical constraint when it comes to horizontal delimitation (unlike in the

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[11] To bring home this point, look at Ghiselin's (1997, p. 1) remark: "When does human life begin? Never, for it is part of an unbroken series of generations that goes back to Darwin's warm little pond". An analogous question within the human species would be when one's own family came into being—ultimately, all our pedigrees go back to the same first human population ("Adam and Eve", as it were).

vertical dimension), similarity can and perhaps must be used as an operational guideline. And whether legitimate or not, in taxonomic practice, this is what has been done for centuries or even millennia. There is a growing awareness of including as much biologically relevant data as possible from as many disciplines as possible (morphology, genetics, physiology, ecology, behavioural biology, etc.) to arrive at a truly "integrative taxonomy" (Tautz et al. 2003; Dayrat 2005; Will et al. 2005; Padial et al. 2010; Galimberti et al. 2012). But however much independent data one has produced[12] and however well-designed species delimitation algorithms are, the question if two populations are classified as a single or as two distinct species ultimately always boils down to whether they are "sufficiently similar" or "sufficiently distinct", respectively. Two analyses with a particular focus on botany on how species are delimited in published scientific articles and monographs came to the conclusion that (1) often the species concept or delimitation method is not explicitly stated and (2) morphological differences, i.e. level of similarity, are by far the most common criterion, implicit or explicit, to delineate species boundaries (Luckow 1995; McDade 1995). Both authors also stress that the theoretical underpinning on which researchers base their decisions should at least be explicitly stated. Although these two studies are more than 20 years old and were biased towards botany, there is little doubt that their results are overall still valid (see Pante et al. 2015), as I can also confirm from my own experience as editor-in-chief of a mammalogical journal that frequently receives articles in which new species are described or existing species split. Our publication policy (Zachos 2016) is that explicit reference must be made to the species concept according to which new taxa are introduced, and we discourage erection of species based on superficial data such as simple morphometric differences, single-locus molecular phylogenies (especially if based on mtDNA only; see also Dávalos and Russell 2014) or arbitrary values of genetic distance. My personal opinion is that the null hypothesis should be conspecificity of closely related populations, but working largely on intraspecific variation I freely admit to being potentially biased here. Published opinion is expectedly heterogeneous on this topic. Meiri and Mace (2007), Carstens et al. (2013) and White (2014) argue for a cautious or conservative approach to species delimitation because "failing to delimit species is preferable to falsely delimiting entities that do not represent actual evolutionary lineages, particularly when the goal of the analysis is species description" (Carstens et al. 2013, p. 4376). It must be emphasized once more, though, that even if all entities under study are evolutionary lineages, species delimitation is not unambiguous (see Sect. 6.1). There are also authors who explicitly place the burden of proof on lumping and advocate a null hypothesis of different species status until rejected (one example for bird species is Gill (2014) who also recommends to treat divergent allopatric taxa as distinct species by default). Either way, similarity is not the villain as which it has been portrayed so often when it was rejected as an alleged resurrection of

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[12] Overall, it seems that most species are still described based on data from single disciplines, mostly morphology (Pante et al. 2015).

"typology". In a sense, then, we are all "typologists" as we all rely on similarity to some degree, not only in our innate ways of categorizing the world around us but also when it comes to scientific taxonomy. Similarity is indispensable; what is important is to not grant it a role that it cannot and must not play in the light of the theory of evolution. Similarity cannot define species status, it can only be used to identify species and to arrive at a ranking criterion that tells us how inclusive the natural entity that we call species should be. Accusing everyone arguing with similarity of "typology" is not helpful. It is also dishonest as we all have to resort to similarity sooner or later. At the very least, the use of similarity as a ranking arbiter *in accordance* with genealogy (i.e. ultimately history) should not be vilified. When the two clash, however, genealogy must be given priority in order not to disrupt historical entities for the sake of likeness.

Because species delimitation is a fuzzy business, and because what constitutes "sufficient distinctness" or "sufficient similarity" for distinct species status or conspecificity, respectively, is a potentially very subjective judgment, the best we can achieve and should aim for is as little subjectivity as possible. We would then not be left with a Taxonomic (or Cynical) Species Concept that leaves the decision up to any competent taxonomist, but could arrive at least at a "consensual" species (delimitation) concept.[13] The only way this is possible is through a standardized approach at species delimitation. This guarantees that species status is assigned in a repeatable and falsifiable and in this sense objective way, but it is important to realize that it is objective only with regard to whether the chosen criteria are met; the choice of these criteria necessarily involves an element of arbitrariness: as said before, an arbitrarily chosen threshold that can be measured objectively is not the same as an objective delimitation criterion.

A recent attempt at a standardized way of delimiting species comes from ornithological taxonomy, the so-called Tobias criteria. Tobias et al. (2010) introduced a quantitative framework and taxonomic scoring system to allow for an evidence-based repeatable way of assigning species status. The underlying data are from five classes of taxonomic character: morphology (biometrics), acoustics, plumage and bare parts, ecology and behaviour and geographical relationships. The difference in pairwise comparisons of populations for each of the five classes is measured and quantified based on statistical effect sizes or qualitative scores (e.g. for geography: broad hybrid zone, narrow hybrid zone, parapatry, allopatry). The result is "a simple point-based system whereby phenotypic differentiation between taxa is scored according to four degrees of magnitude (minor, medium, major and exceptional). These categories are defined, as far as possible, according to quantitative thresholds [. . .] Overall divergence is then summed and compared with that found in irrefutable species" (Tobias et al. 2010, p. 731). The threshold

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[13] A similar idea is advocated by Hey (2001a, b, p. 188) who says that "because of the large human component of our taxa [. . .] we must prepare ourselves to accept [. . .] that a species taxon is what systematists agree it is". See also Heywood (1998) and Seifert (2014); the latter's Pragmatic Species Concept also includes "consensus among the experts of a discipline" (p. 89).

sum for distinct species status is a score of at least 7. The method is quite elaborate, also statistically (using effect sizes, not simple p-values), but the details are not relevant in the present context. Perhaps surprisingly, genetic data are not included, but in theory they could be. The reason they are not at the moment is mainly that they are not as widely available as phenotypic data, and the authors want their system to be applicable ideally to all avian taxa. The system by and large works under a flexible version of the Biological Species Concept and evaluates allopatric taxa based on a comparison with divergence in sympatric or parapatric taxa, but that it is a doubtful approach (see Sect. 5.3). Nevertheless, it is, to my knowledge, the only framework of its kind so far and deserves merit for that because consistency is greatly enhanced. It might pave the way for similar approaches for other taxa or might even be adopted, with minor modifications, for some, e.g. frogs, toads, cicadas or some mammals (Brooks and Helgen 2010). The Tobias criteria have been implemented, together with a quite detailed discussion on species concepts and species delimitation in the introductory section, in the *Illustrated Checklist of the Birds of the World* (del Hoyo and Collar 2014), but unlike Tobias et al. (2010), who reported little taxonomic change when they applied their system to 23 pairs of European bird subspecies, the authors have now arrived at 462 additional species through splitting as opposed to 30 fewer through lumping, which has been criticized as taxonomic inflation (Cheke 2015). Overall, however, it has been hailed as progress: "This system will not make species delimitation wholly objective, but it is a substantial step forward. [. . .] there is a great advantage to be had in standardizing evaluations of differences across multiple character suites. Critics might focus on the method's subjectivity and the fact that its quantitative basis rests upon somewhat arbitrary magnitudes of difference. However, by demonstrating repeatability, by rendering what have historically been idiosyncratic judgment calls (albeit usually by experts) into a quantitative framework, and by insisting that multiple diverse character suites have been sampled, the authors firmly place a degree of consistency and transparency upon taxonomic decisions, and this will be widely welcomed" (Winker 2010, p. 681; see Brooks and Helgen (2010) for another favourable evaluation).

Finding a one-fits-all system of criteria for all living organisms seems unlikely given the enormous diversity of life. But something like the Tobias criteria, complemented by genetic data, might be our best candidate. Elements from Templeton's Cohesion Species Concept, in particular the evaluation of demographic or ecological exchangeability, might be helpful when dealing with allopatric populations. But the more divergent the frameworks for different taxa are, the more doubtful it becomes whether species taxa across the Tree of Life are really the same. Rather, then, what we call by the same name ("species") may in reality be apples and oranges. We may simply have to accept the fact that our classifications will always be like a photograph with limited resolution: if we do not zoom in too much, the picture will represent real natural patterns, but the more we zoom in, the blurrier and more artificial our picture will be. Unfortunately for us, this fuzziness is located right around the level of (closely related) species and that has important consequences if we want to use species as the common currency in ecological and evolutionary research. To this issue we now finally turn.

Chapter 7
The Practical Relevance of Species Concepts and the Species Problem

So far we have mainly dealt with the species problem from an academic perspective—how species notions have evolved historically, what ontological or metaphysical status species have, what species concepts there are and how they differ and why, etc. It was only in the last chapter on species delimitation that taxonomic practice was given more attention, although the focus was on general issues and again theoretical arguments. The main conclusion was that species delimitation will necessarily contain an element of arbitrariness because of the continuousness of the phenomena and processes underlying the origin, distribution and evolution of biodiversity. As a result, the discrete, binary nature of taxonomy (taxon or no taxon) cannot adequately and completely objectively capture and classify diversity at and around the level that we usually think of as species—i.e. the level at and around the tokogeny/phylogeny divide (in sexual organisms) of closely related populations that may or may not be fully interfertile, may or may not merge again or may or may not exchange genetic material or may or may not show close phenotypic affinities and sometimes hybrid zones of varying geographical extension and degrees of permeability, etc. Nevertheless, species are commonly viewed as the main currency in many areas of biological research, both applied and theoretical. What impact does the insight that species boundaries cannot be drawn completely objectively have on these disciplines? This will be briefly summarized in the present chapter. The aim is not to provide detailed analyses of how species uncertainty bears on concrete research questions but to give an overview of what is at stake and to sensitize readers to this important issue.

7.1 The Power of Names: "Taxonomy as Destiny"?

> "*Whether we like it or not, the species rank has a special resonance with the public and with policy-makers*." Georgina Mace (2004, p. 711)

F.E. Zachos, *Species Concepts in Biology*, DOI 10.1007/978-3-319-44966-1_7

In 1975, a most curious paper was published in the journal *Nature*. In it, Sir Peter Scott and Robert Rines (1975) give a formal species name to Nessie, the Loch Ness monster: *Nessiteras rhombopteryx*.[1] The rationale behind this unusual taxonomic effort is the following: while the existence of Nessie may be uncertain, if indeed it does exist, it exists in small numbers and deserves protection. And to be protected it must have a taxonomic name. Names are important—very concretely when it comes to legal protection, but also in a less tangible way by increasing the awareness that a population or a group of populations is indeed unique. With respect to Nessie, Scott and Rines (1975, p. 468) therefore conclude that "giving the species a name will not only provide it with the necessary protection but also focus greater attention on further studies". And it is for this reason that having a name can make the difference between survival and extinction.

The quote in the heading of this subchapter—"Taxonomy as destiny"—is the title of a commentary (May 1990) on a publication on the effects of taxonomy on extinction risk in tuataras (*Sphenodon* sp.), the sole survivors of an ancient reptilian lineage and divergent extant sister taxon to lizards and snakes (Squamata). In it, Daugherty et al. (1990) argue that the lumping of all living tuatara into a single species (*Sphenodon punctatus*) has contributed to the near-extinction of a subset of tuatara that they consider (and that used to be considered) a distinct species, *S. guntheri*: "Perceived monotypy of tuatara apparently forestalled management intervention on behalf of threatened populations" (Daugherty et al. 1990, p. 177). Whether or not the specific status in this particular case is warranted, there is no doubt that having a taxonomic name, and also whether a population is classified as a subspecies or a "full" species, can make a potentially decisive difference when it comes to protection and awareness. Accordingly, this matter and the way different species concepts bear on the issue have been discussed in quite some detail (e.g. O'Brien and Mayr 1991; Geist 1992; Isaac et al. 2004; Mace 2004; Haig et al. 2006; Garnett and Christidis 2007; Marris 2007; Morrison et al. 2009; Frankham et al. 2012; Gutiérrez and Helgen 2013; Zachos et al. 2013b; Senn et al. 2014). Particularly the publication by Isaac et al. (2004), which coined the term "taxonomic inflation" for the increase in species numbers due to the raising of existing subspecies to species level, triggered a number of comments, rejoinders and subsequent rebuttals (Agapow and Sluys 2005; Harris and Froufe 2005; Isaac et al. 2005; Knapp et al. 2005; Mallet et al. 2005; Groves 2014). How big an impact taxonomy has on conservation decisions in general and not just in specific cases is not so clear, however. Garnett and Christidis (2007) give a nice overview of definitions of species or their equivalent for a number of international conventions and legislation such as the Convention on Biological Diversity, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the US Endangered Species Act. They conclude that "most laws and international

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[1] The name literally means "Ness monster with diamond(-shaped) wing" and is an allusion to its alleged similarity with something like a plesiosaur. Incidentally, it is also an anagram of "monster hoax by Sir Peter S".

conventions avoid arguments over species' definitions altogether, thus negating arguments that such definitions should be changed to further species' conservation" (p. 187). Yet, they also say that "[a]lthough the legal implications of changing species definitions may be surprisingly small [...], each time the name of a species changes, or species boundaries are redefined, a huge bureaucratic process is triggered to update schedules, regulations, maps and publications. This has both transaction and opportunity costs, the former because substantial conservation monies are spent negotiating the new lists through the administrative processes, and the latter because those funds might have been available for genuine on-ground conservation" (p. 189). In itself this is no argument against either taxonomic changes or conservatism (which the authors emphasize), but it highlights that taxonomic changes do have consequences and that species boundaries are not just of academic interest. Morrison et al. (2009) carried out a qualitative study, simply looking for examples where taxonomic change had a positive effect on conservation efforts (due to splitting and taxonomic recognition), where it had a negative effect (through lumping and subsequent lack of protection) and where it had none. They found examples for all three and no evidence of a consistent effect of taxonomic changes on conservation. They also suggest that name changes have the least effect when charismatic organisms are affected: "Populations valued by humans, for whatever reason—charisma, beauty, or economic worth—are protected regardless of their taxonomic rank" (p. 3205). At present, perhaps the most (in)famous example of how important names can be beyond the realm of biology is the California gnatcatcher (*Polioptila californica*), a little insectivorous songbird. More precisely, it is about whether the threatened coastal California gnatcatcher should be classified as a distinct subspecies (*P. c. californica*) or not. At present it is, and keeping up this classification would entail particular protection of this bird and its habitat, the coastal sage scrub, under the US Endangered Species Act. This habitat contains potential real estate of enormous economic value, and if subspecies status were denied, the coastal sage scrub population would be just another *P. californica* population and would not be entitled to special protection. Because of the big money involved, the issue has received considerable attention in the media. Two studies, based on mitochondrial DNA (Zink et al. 2000) and nuclear DNA as well as ecological niche modelling to test for niche divergence as a proxy for ecological distinctiveness of the coastal California gnatcatcher (Zink et al. 2013), did not produce evidence in favour of its taxonomic recognition as a subspecies, but the results have been criticized as being inconclusive (McCormack and Maley 2015). The issue has thus not been settled, but it also highlights, as Zink et al. (2000) emphasize, that it is risky to rely on a single flagship species when it comes to conservation efforts for threatened habitats. The value of the coastal scrub sage does not hinge on whether the coastal California gnatcatcher is distinct or not; it is a threatened ecosystem with endemic species, and "preservation of the California Gnatcatcher should be coupled to preservation of the coastal sage scrub ecosystem, rather than the reverse" (Zink et al. 2000, p. 1403).

The gnatcatcher example was based on subspecific classification (see also the Mesola red deer *Cervus elaphus italicus* in Sect. 5.9), but the very same applies to the species level.[2] Of course, one could now ask, given that species delimitation is a grey area in many cases and given that a name might have beneficial consequences, why splitting should not be the rule rather than the exception, at least in cases where neither splitting nor lumping seems to be favoured by existing data. First of all, this is often done anyway, and not only with an eye on conservation but simply based on a certain taxonomic philosophy (e.g. adherence to a Phylogenetic Species Concept). Secondly, there are other things to keep in mind, too. Splitting leads to more species that have smaller population sizes than the more inclusive species did that has been split. Different species must be managed separately, so that introductions of (formerly) conspecific individuals into small and isolated populations that have undergone high levels of genetic drift and depletion (and are often diagnosable because of this so that they would qualify as distinct species under the dPSC) may now require the mixing of two different species. The ensuing legal and regulatory ramifications could well preclude such a "genetic rescue" approach,[3] meaning that "splitting, sometimes in an attempt to promote greater conservation of biodiversity, can actually prevent conservation actions necessary to preserve taxa with a small population size, and thereby result in greater loss of existing biodiversity" (Frankham et al. 2012, p. 27; see also Zachos et al. 2013b). This may be particularly relevant in the case of captive breeding programmes which are usually based on small populations anyway. More different species will also lead to a higher number of organisms and populations that are considered interspecific hybrids whose legal protection status is often unclear (see the discussions about the red wolf *Canis rufus*, which is believed to be the result of hybrid speciation between grey wolves and coyotes). Splitting of, for example, ungulates might even create new target species for trophy hunting (both legal and illegal).

A further point is that of biologically meaningful units. This is of course a highly subjective concept, but the criticism that the approach to defining evolutionarily

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[2] That this issue is indeed of practical relevance can be seen, for example, by how seriously the issue of species splitting is taken by the United Nations Environment Programme's World Conservation Monitoring Centre (UNEP-WCMC 2012). In this document, the recent species splittings in many groups are highlighted, among them primates and bovids.

[3] Genetic rescue is the introduction of unrelated individuals into a small and isolated population that is genetically depleted and may show signs of inbreeding depression—with the aim of supporting the local gene pool and decreasing the level of inbreeding. The textbook example is the mountain lion population in Florida ("Florida panther"). It is usually classified as a distinct subspecies (*Puma concolor coryi*) and was on the brink of extinction with serious signs of inbreeding depression (low sperm quality, genital malformations and other symptoms). Finally, in 1995, eight female Texan pumas (*P. c. stanleyana*) were introduced and the population has recovered well (Johnson et al. 2010). However, there was also opposition to the genetic rescue because it would dilute the original Florida panther gene pool. This opposition (and legal hurdles) would have been even stronger if the Florida panther had been classified as a distinct species, and this may well have resulted in its extinction.

significant units (ESUs) for conservation purposes based on neutral molecular markers neglects ecological and adaptive significance can be applied to the species level, too.[4] Under the diagnosability version of the Phylogenetic Species Concept, many species will be recognized that differ in traits that are in all likelihood biologically trivial, e.g. single base pairs in sequences of the cytochrome b gene as in the case of Sumatran tigers (see Sect. 5.6.2). They are diagnosably different, that is a biological reality, but is it the biological reality that we think of when we choose the species level as the unit of biodiversity worth protecting? There is no right and wrong here, but I think that many biologists and conservationists would answer this question in the negative. Recognizing many species where there was hitherto only one may also have a psychological effect: just like in economy, inflation in taxonomy causes devaluation, among scientists and the public, and this will probably be more so if species differences are perceived as trivial. Agapow et al. (2004) have (conservatively) estimated an increase in species numbers across taxa of at least 48.7 % based on the application of the Phylogenetic Species Concept (s). This also leads to an increase in threatened species because of the concomitant reduction in individuals per species and species ranges which are two of the criteria for the IUCN Red List classification. The number of mature individuals would on average decrease by 32.8 %, which in turn would, for example, be equivalent to a reclassification of 10.9 % of all “Vulnerable” species in the Red List as “Endangered”.[5] The authors also estimate the increase in costs for a full recovery of all species listed in the US Endangered Species Act. This figure would increase from around US$4.6 billion to about US$7.6 billion.

It is important to realize that both unwarranted splitting and lumping can have detrimental conservation effects. The newly discovered *Vipera walser* (see Sect. 6.4) was erroneously lumped with the common adder,[6] and only now do we know about its uniqueness and can take appropriate measures to protect it. Although I am personally more inclined towards lumping, the aim of this chapter is not to malign splitting and advocate lumping. It is to point out that the fact that we give unique names to some groups but not to others and that the theory and evidence upon which we base these decisions both have relevant ramifications for the conservation and management of biodiversity. This we should be aware of when we make use of taxonomic information or when we revise the taxonomy of a group.

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[4] Cracraft (1997, p. 325), incidentally, says: “Phylogenetic species, as basal diagnosable units, are effective functional equivalents of ESUs”.

[5] Based on the assumption that the numbers of mature individuals in “Vulnerable” species are evenly distributed throughout the range of possible values for this category (250–1000).

[6] In this case it is not an issue of where to draw the line in a continuum, but of an objectively wrong classification because two unrelated lineages were lumped into a polyphyletic species.

7.2 Species as the Currency in Biodiversity Research and Evolutionary Biology

Species are often used as the basic unit in a variety of applications, most notably so in biodiversity and evolutionary research. In fact, when asked about biodiversity, most people will think of species numbers. For example, one of the simplest measures of species diversity is species richness, which is just the number of different species in an area or assemblage of organisms under study. Actually, even this measure is not as simple as it may seem as it is influenced by, for example, sampling effort and abundance (Gotelli and Colwell 2011; Chap. 3 in Magurran 2004). But the important point here is that of course species richness is also a function of the underlying species concept. Counting species based on the diagnosability version of the Phylogenetic Species Concept will yield different numbers from counts based on the Biological Species Concept or the Phenetic Species Concept. What exacerbates this further is that usually one does not count all species anew when making an inventory. Rather, one relies on published work by others, either completely or for single groups. Different authors working on different groups will use different species concepts, and even if they don't, they are likely to differ in where exactly they draw the boundaries nonetheless so that what is seemingly objectively subsumed under the same name of "species" may be very different entities after all. This is a kind of species pluralism in practice: what has the same rank in our classifications (T species) may be equivalent to different kinds of species or different levels of lineages in the Tree of Life, leading us to compare apples and oranges, or rather lump them in the same analysis of what we think pertains to a single kind of fruit. In this case Heywood (1998, p. 211) would be right when saying that "[s]pecies are equivalent by designation, only not in terms of their state of evolutionary, genetic or ecological differentiation or divergence". The use of species as basic units in ecology and biogeography has been questioned on these grounds, e.g. by Riddle and Hafner (1999) who recommend to use evolutionarily significant units instead (ESUs are, however, not unproblematic either; see Sect. 5.9). Similarly, Hendry et al. (2000, p. 73) conclude that "any study comparing species numbers among taxa, geographical regions, or time periods obscures the fact that biological diversity is poorly quantified simply by counting the number of taxonomic species."

Let us look at two concrete examples. Peterson and Navarro-Sigüenza (1999) comparatively analysed the level of endemism and the distribution of endemic species of birds in Mexico based on the Biological Species Concept and the Phylogenetic Species Concept. They found 101 endemic biological and 249 endemic phylogenetic species. Importantly, their geographic distribution differed considerably so that the designation of conservation areas based on avian endemism critically depends upon which of the two species concepts is used. Meijaard and Nijman (2003) arrived at similar findings in a study on Bornean primates, again comparing the Biological and the Phylogenetic Species Concept. While the identification of hotspots of primate species richness was not affected by the underlying species concept, the location of endemic primate species hotspots was. Single-taxon analyses to locate diversity hotspots can therefore produce very different results when different species concepts are used. While perhaps more inert in this regard, multi-taxa studies in principle suffer the same shortcoming. One of the most influential approaches to defining areas or regions of conservation priority is that of biodiversity hotspots. In its narrow-sense technical definition, a biodiversity hotspot is a terrestrial area of outstanding irreplaceability and vulnerability that harbours at least 1500 endemic vascular plant species (equivalent to 0.5 % of the ca 300,000 known species; irreplaceability criterion) and 70 % of whose primary vegetation has been destroyed (vulnerability criterion) (Myers et al. 2000; Mittermeier et al. 2011). There are, at the moment, 36 areas that meet these two conditions (Mittermeier et al. 2011; Williams et al. 2011; Noss et al. 2015) and that therefore should be prioritized when it comes to the question where action towards the reduction of biodiversity loss should be directed first.[7] The concept has been very successful—it has been estimated that more than US$1 billion have been focused on conservation in these biodiversity hotspots (Mittermeier et al. 2011). The 36 hotspots combined undoubtedly harbour a large proportion of the earth's biodiversity, but one of the two cut-off criteria for inclusion is a species count, and such counts may not be entirely objective.[8]

Many approaches to conservation do not rely on simple species counts. A popular approach is that of including phylogenetic diversity in its broadest sense, which means that not all species are treated equally but that they are weighted according to their evolutionary distinctiveness, i.e. how divergent they are from related species (e.g. Vane-Wright et al. 1991; Faith 1992; Hendry et al. 2000; Cadotte et al. 2010; Davies and Cadotte 2011; Vellend et al. 2011). The fewer close relatives of a species are still extant, the higher the score of phylogenetic diversity. Divergence can be measured, for example, based on branch lengths in an evolutionary tree. The idea behind this approach is that very divergent species represent a larger fraction of a group's overall evolutionary history or legacy. For example, the extinction of a divergent and phylogenetically isolated[9] species such as *Welwitschia mirabilis* or the platypus would be a "more unique" loss than the extinction of, say, a single species of a species group like that of dandelions (*Taraxacum* sp.). The inclusion of a measure of phylogenetic diversity thus adds an element of something analogous to disparity (the extent of occupied character

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[7] There are other approaches that result in different areas or regions, of course, but this is irrelevant for our context.

[8] A different problem is that even if species taxa across all groups were objective and directly comparable, one group's diversity in an area may not be representative of that of other groups. While key to the successful protection of overall biodiversity, this issue is not relevant to our present topic as it regards intergroup differences in diversity distribution but not the delimitation of species.

[9] Divergent and phylogenetically isolated in this case means that the summed branch length to a species' sister taxon is very high. Branch lengths can of course be measured differently, but ultimately they are a function of time to common ancestors.

space, usually morphospace; Gould 1989) to simple measures of diversity (number of species).[10] This rationale has been implemented, for example, in the conservation of mammals (and subsequently other groups) in the so-called EDGE approach (Isaac et al. 2007). EDGE stands for *E*volutionarily *D*istinct and *G*lobally *E*ndangered and combines evolutionary distinctiveness (ED, a particular quantification of phylogenetic diversity based on branch lengths) with the level of extinction risk based on the IUCN Red List categories. Not surprisingly, the top three EDGE mammals are all monotremes (highly divergent) and more particularly three long-beaked echidnas (*Zaglossus* sp., all three classified as Critically Endangered). What is important to notice here is that the weighting of species in these approaches is *not* an argument against the objectivity of the species rank. Even if all species had the same age (i.e. the same time to their and their sister species' last common ancestor) and the same amount of phyletic evolution had occurred in each species lineage, extinction of species would result in the "phylogenetic isolation" of others, making them different with respect to their evolutionary distinctiveness. Yet, this is no reason for complacency because there are still many reasons to at least doubt that all species taxa, even only the sexually reproducing ones, are really the same thing.

Biodiversity is also often quantified in evolutionary studies. Again, the basic unit most often used is the species. In fact, it has been argued that one should use species because the use of higher categories, due to their arbitrary delimitation, will lead to spurious results. This so-called taxonomic surrogacy, replacing species numbers with those of higher ranks, is indeed known to produce results that are dependent upon subjective rank assignments (Allmon 1992; Bertrand et al. 2006). It is very common in palaeontological studies to compare biodiversity through time and infer diversification rates, extinction events, etc., and it is not unusual to base diversity quantifications on higher taxa. Stanley (1979, Chap. 5) compares diversification rates of mammals and bivalves based on families of the two groups. He does this quantitatively, but the use of units that are subjectively delimited ("families") makes this approach seriously flawed. Allmon (1992) gives a nice figure of diversity of the Turritellidae (Gastropoda) based on different delimitations of genera, and it becomes clear that this kind of analysis will only yield a very rough and qualitative idea of how these groups diversified through time. The use of higher Linnaean categories as proxies for general diversity will always yield doubtful results, but the worrying question is if species are really so much different in that regard. For example, Faurby et al. (2016) have used simulation analyses to test for the impact of different taxonomic decisions at the species level (splitting vs lumping) on diversification analyses. They specifically implemented different taxonomic philosophies in different subclades, and they have shown that splitting and lumping does affect the results and the conclusions pertaining to macroevolutionary patterns. The authors are, wisely, cautious in interpreting their results (which differ

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[10] Fortunately, the above-mentioned biodiversity hotspots do not only harbour extraordinarily high numbers of species but seem to also harbour high levels of evolutionary history or phylogenetic diversity (Sechrest et al. 2002).

for different metrics), and they "recommend that the reader focuses on our qualitative finding, rather than any specific quantitative result", but they emphasize that "[c]aution is especially warranted under two different scenarios; (1) if a shift in diversification rate is inferred for a node separating clades that have been treated by different taxonomists, and (2) if one or more shifts in diversification rate are identified very close to the tips of the tree, that is potentially at the point where populations shift between being separate species and intraspecific populations" (Faurby et al. 2016, p. 12).

While Faurby et al. (2016) focused on inter-taxonomist differences and the ensuing effects on evolutionary analyses, it is important to keep in mind that even a single taxonomist is no guarantee for species being delimited consistently, simply because there is no completely non-arbitrary cut-off criterion when it comes to cutting up a continuum. Species like leopards, red deer or black kites have a huge distribution range and live in a variety of very different habitats, which makes them prime examples of ecologically very plastic species. However, if they are split into different species (as has been done, at least for red deer and black kites), the resulting species are much less plastic ecologically. The decision of where to draw the lines in the grey area around the species level—a situation where ultimately different decisions are equally right or wrong—determines our ecological raw data. If we carry out a meta-analysis on many species, we might well end up in a situation similar to the one highlighted by Allmon (1992) for turritellid genera where the very decision on how to draw category boundaries was the most important factor in determining the final result. There are probably few very widespread species that could not be split based on some species identification criterion. For example, there are many Holarctic taxa that are either classified as a single species or as two species, a Palaearctic and a Nearctic one.[11] There are countless examples, among them grey wolves, red foxes, moose, reindeer, brown bears, golden eagles, grey/blue herons, great grey owls, Tengmalm's owl, northern hawk-owl, three-toed woodpeckers, ravens and many more, also from other taxa than mammals and birds.[12] All of these species pairs are potential error sources in analyses based on species entities. For analyses based on species, and particularly species numbers, to be scientifically sound, we have to be sure that all the species taxa in our analyses not only carry the same designation but really are the same kind of thing. If that is

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[11] I am not considering the fact that many could also be split further *within* Eurasia and North America, respectively, which adds to the taxonomic uncertainty.

[12] Just a few comments here. The three-toed woodpecker is an example where recently splitting has been suggested such that only the Eurasian populations go by the name of *Picoides tridactylus*, while the American three-toed woodpecker is called *P. dorsalis* (Zink et al. 2002). Grey and great blue herons are usually considered two species (*Ardea cinerea* and *A. herodias*), while wolves (*Canis lupus*) and brown bears (*Ursus arctos*) are considered conspecific. Red deer and wapiti used to be classified as the same species, but recently splitting into two species (*Cervus elaphus* and *C. canadensis*) has been more common. The important point here is not so much what the common taxonomic view is at any one time, but rather that for the majority of these taxa pairs both splitting and lumping could be argued for, depending on the criteria that one considers most relevant.

not the case, then there is no such thing as an objective species category, or at least we have not yet found it. There are authors who think that exactly this is the case (see Sect. 3.6 for references and details), and if they are correct, then the only painful conclusion to be drawn from this would be that "the species must continue to be defined pragmatically by practising taxonomists in the way that most effectively divides the group of organisms in question into units which it is useful to recognize and name, bearing in mind the needs of the various user groups. Comparisons across classes of organisms in terms of species must be treated as no more than general indications of amounts of biodiversity, not as precise statistics" (Heywood 1998, p. 211). In line with this, Hendry et al. (2000, p. 74) think that "the species paradigm can be profitably replaced with a system based on the quantitative description of variation within and among groups (or clusters) of organisms."

Jody Hey, who is always aware of the discrepancy between named species taxa and real evolutionary entities (T species vs E species), thinks "it is folly to suppose we might have consistent taxon counts on an absolute scale. But there are contexts where we can have consistency and where counts of taxa, including species taxa, are useful" (Hey 2001a, p. 187). He goes on to say that consistency among taxonomists can be reached by introducing common methodology (see also Mace 2004 and the Tobias criteria in Sect. 6.4) which could result in repeatability of species counts, although "such methods would necessarily be largely arbitrary, at least with respect to real species" (i.e. E species). But the "genuine problem with species counts, even repeatable ones that are arrived at with a consensus on methods, is that we don't know just what they are counts of" (Hey 2001a, p. 187). Still, even though such numbers do not correctly reflect underlying natural patterns, standardized species counts can be valuable in assessing changes in these patterns. A change in the real number of evolutionary entities (E species) will also result in a change of our partly artificial standardized T species numbers: "Thus, even though the absolute counts in these contexts may not have the meaning people often assume of them, the changes in such counts actually do reflect changes in the amount of biological diversity" (p. 187f.). In that regard, species would then be very much like higher taxa. We should remember what Doolittle and Zhaxybayeva (2009) said about prokaryotic species, and what applies perhaps similarly to eukaryotic species—that there might be "no principled way in which questions about prokaryotic species, such as how many there are, how large their populations are, or how globally they are distributed, can be answered" (p. 744) but that, importantly, this disappointment "is no excuse for forcing a conceptual straitjacket on unruly data" (p. 754). A disappointment indeed, but maybe true nonetheless. According to Hey (2001a, p. 189), the "broad human interest in the quantity—we can call it S—of the number of real species, out in nature, is quite a phenomenon. The S notion [...] is an integral part of a great deal of discourse on biological diversity, among professional biologists and laypersons alike. It is a mountain of a tradition and will probably not be shifted any time soon, even though S is a chimera. Biologists are right to try for consensus on methods for recognizing taxa, and for counting the taxa they recognize, for such numbers can be used to track changes and to make comparisons among different geographical regions. But the sooner we recognize that taxa lie partly within us, and the sooner we stop dwelling on S and other hypothetical absolute counts of species taxa, the better scientists we will be" Hey (2001b).

Approaches based on relative changes rather than absolute numbers are actually not so uncommon. Effective population size, for example, the size of an idealized population with the same rate of loss of genetic diversity as the real population under study, is notoriously difficult to estimate. There are a number of approaches, e.g. based on genetic data (Luikart et al. 2010), but there are many unknowns in these calculations, so that the results are best interpreted in a comparative context rather than viewed as reliable absolute numbers.[13] Similarly, population viability analyses (PVAs) are critically dependent upon data on life history, demography, ecology, habitat variables, etc. Often, these data are not or only partly available, and absolute results, e.g. for extinction probabilities, will therefore be prone to error. However, one can conduct so-called sensitivity analyses to infer which parameters (poaching, inbreeding, carrying capacity, etc.) have the largest relative impact on population viability (e.g. Wisdom and Mills 1997). This information can then be used to direct conservation resources towards where they are most needed and most efficient. Perhaps ultimately species counts should be treated in the same way.

7.3 Concluding Remarks

Is a lion the same kind of entity as a tiger? Perhaps. But what about a lion and a species of weevil or moss, let alone bacterium? That species counts—and indeed any analysis treating species taxa as the same kind of thing, implying that the species category is objectively real—might be seriously flawed is a worrying prospect. There is evidence that they often are, although we have no way of knowing how flawed they are. On the other hand, I am not aware of an analysis that specifically addressed this problem and came up with the relieving result that all is fine and that species taxa are directly comparable. Nor do I know how such a study could be performed. I have become much more critical towards the idea of a truly objective species category, and even if it exists, I am sceptical that our classifications will ever be a good representation of it given how little we know about the large majority of life forms on earth. Most species are understudied or not even studied at all. Assuming that the T species of our monographs and reference lists actually match real evolutionary entities in most cases seems to me more and more like a naïve act of wishful thinking. If an objective species level exists, i.e. if

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[13] In a study of European red deer, we have done exactly this (Zachos et al. 2016), and the bottlenecked and threatened populations/subspecies of red deer on Sardinia and in Mesola were found to exhibit by far the lowest values, often one or even two orders of magnitude lower than those for other populations. Still, the absolute numbers may not be very reliable.

species category nominalism is wrong, then there might be more than one such level, either different ones for different taxa (e.g. sexual vs asexual groups) or different ones depending on what kind of lineages one is interested in. This kind of species pluralism would mean that horizontal species delimitation would be more inclusive based on one kind of objective species level (perhaps based on interbreeding) than on another (perhaps based on ecological niches). I have my doubts whether this second kind of species pluralism is warranted, but perhaps biologists are less prone to accept it than philosophers because they actually have to live with the practical ramifications that potentially ruin many lines of research that we have come to hold dear. Having discussed and criticized so many views on species in this book, it is perhaps only fair to unclose my own fallible views as well. The more I have read and thought about the species problem, the less I seem to know, and whenever I read authors who are confident and, at least seemingly, absolutely certain that they have it right, I am half impressed and half incredulous. I do believe that species taxa are real and that they are historical individuals in a philosophical sense. Of this, I think, there can be little doubt (but I might still be wrong). I also think that they are lineages, and that the Evolutionary Species Concept and the General Lineage or Unified Species Concept with their notion of a hierarchy of primary species concepts and secondary species criteria are a biological breakthrough. I do think that the tokogeny/phylogeny divide in sexual organisms is the best candidate for a real species level and thus for an objective species category, but the grey area when it comes to delimiting species is unfortunately rather wide. This introduces a necessary element of arbitrariness to the species category because it means that not all species taxa are exactly the same. As a consequence, not even if we knew everything there is to know about all life on earth would we be able to arrive at a completely non-arbitrary classification. In the real world, where we are far away from biological omniscience, the discrepancy between T and E species will in many cases be such that what we call species is really nothing but a name. How deeply this affects our research in ecology, biodiversity and evolution I have no way of knowing, but my guess would be: more than we are aware of.

Chapter 8
A Brief Summary of the Book

Perhaps the single most important message of this book is that boundaries in nature are fuzzy. The Tree of Life is a fractal pattern with lineages nested within lineages. "Carving up nature at its joints" is therefore a messy business. Also, many phenomena relevant to species definition and delimitation (such as interbreeding, sexuality, similarity, allopatry, etc.) are continua, making concrete cut-off criteria within a grey area necessarily somewhat arbitrary. Much of the confusion we are facing with species is therefore an authentic representation of nature's underlying fuzziness. Taxonomy is a discrete ordering system imposed upon the continuous (and fractal) structure of the Tree of Life. A perfect match of the two is impossible.

The species problem is a complex of different issues. First and foremost it refers to the fact that there are different inconsistent ways of dividing biodiversity into species based on different species concepts. It also refers to other problems that we have with species, such as how species should be delimited, whether there is an objective and universal way of defining what species are and how they can be delimited and what species are ontologically (individuals, classes, natural kinds, cluster classes, etc.).

It is important to distinguish between different kinds of uses of the word species. A species *taxon* is a single species, such as *Homo sapiens*, whereas the species *category* is the class of all species taxa. It refers to the level of species in the Tree of Life or the species rank. There is also a difference between the species in taxonomic lists (the taxa that we give binomials) and the underlying natural evolutionary entities that we want to discover. The first can be called taxonomic or T species, the second evolutionary or E species, and the former are at best hypotheses of the latter.

Species can be viewed horizontally, or synchronically, in a cross-section through the Tree of Life at any one time, and vertically, or diachronically, through time. Some authors make an ontological distinction between these two dimensions, others (myself included) think that this distinction is artificial.

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Species realism and species nominalism can refer to both the species taxon and the species category. Species taxon realists hold that species taxa are real, i.e. they exist independently of the human mind, while species taxon nominalists hold that only organisms exist objectively and that species taxa are constructs of the human mind. Species category realism is the position that there is an objectively definable level or rank of species (the species category), while species category nominalists think that different species taxa are not essentially the same thing.

Species and genus are originally logical categories that were introduced into biology via the medieval tradition of Aristotelian logic. It was not until late in the seventeenth century that a purely biological notion of species was introduced by John Ray. According to a popular and widespread view, the so-called Essentialism Story, there was a continuous tradition from Plato and Aristotle until just before Darwin that conceived of species as classes with eternal essences, i.e. necessary and sufficient conditions for an organism to be an element of that class. It took Darwin's evolutionary theory and population thinking to finally overcome this notion. This historical presentation is almost certainly wrong and a fabrication of the twentieth century. There is convincing evidence that pre-Darwinian notions about species were much more diverse and, importantly, much less essentialist. This includes Aristotle himself, whose use of the term species (*eidos* in Greek) in his biological works is very different from that in his logical writings, based on his insight that the living world could not adequately be described by the means of his logic methodology. Even Linnaeus, often presented as the archetype of an essentialist taxonomist, does not fit this category. He may have been an essentialist early on in his career, but he became more and more empirical in his views, and there is no single species concept that we can ascribe to him. Indeed, there have been far fewer true essentialists with respect to species than the Essentialism Story wants to make us believe. Rather, there seems to have been a general awareness that species are groups of organisms that are related through genealogy and produce offspring resembling their parents. This intuitive notion, according to John Wilkins who calls it the "generative conception of species", has been prevalent since at least Epicurean times. The very few exceptions that really thought of species as Platonic ideas with eternal essences include Louis Agassiz. According to this view, Darwin not so much changed the direct notions about species but rather the framework in which species were interpreted. Darwin's own views on species are contentious, particularly with respect to whether he was a species realist or nominalist. When only looking at short quotations without accounting for their context, Darwin's views seem very contradictory, and he may have been uncertain to a degree. The most widespread consensus, although not unobjected, seems to be that he thought that species taxa were real but that the species category may not have been. In the first half of the twentieth century, the modern debate began to take shape, and the prevailing question since has been if and how one can objectively delimit species taxa in such a way that the resulting rank (the species category) is really the same across all taxa and among different taxonomists.

The ontological, or metaphysical, status of species is one of the most contentiously debated issues in the philosophy of biology. It is the question what kind of logical or philosophical thing a species taxon is. Traditionally, species were usually considered to be classes: universals with essential characters, i.e. necessary and sufficient properties for membership of single organisms in a species taxon. Rather than artificial classes created by the human mind, species were mostly regarded as a special kind of class, a natural kind. Natural kinds also have essential properties, but they exist regardless of the ordering human mind as the result of natural causes and laws. The prime examples of natural kinds are chemical elements. But in the 1960s and 1970s, Michael Ghiselin suggested that species taxa were instead philosophical individuals with proper names and without essential properties. They are historical entities with a beginning and an end in time rather than spatiotemporally unrestricted classes or natural kinds. This finally made species taxa compatible with the historical nature of the evolutionary process. There have been attempts at reviving class concepts, e.g. cluster class concepts like homeostatic property clusters or those based on so-called historical essences, and there have also been suggestions to reconcile class concepts with individuality, but most biologists and many philosophers agree that, whatever species taxa may be in addition to individuals, individuality is the most important of their ontological characteristics. An important consequence of species taxon individuality is that we cannot define species taxa based on characters, but that we have to discover them ostensively and that species names are proper names that we give to them in an act of christening (by means of type specimens). An interesting hypothesis to explain why we seem to be prone to conceive of species as similarity classes has been put forward by Jody Hey who believes that our cognitive apparatus is programmed to think in terms of categories that arise as generalizations from recurrent patterns. As a consequence there is a conflict between our scientific insights that species are historical entities and our brains that nonetheless pursue their evolved adaptation of pigeon-holing.

While species taxa are best interpreted as philosophical individuals, the species category is a class—the class of all species taxa—, and the various species concepts are attempts at defining this class. There are ca. 30 such species concepts, and the debates on which is the best one and whether there is indeed a truly universal one-fits-all species concept for all taxa and circumstances are seemingly endless. From a theoretical perspective, a solution has been proposed based on a hierarchical approach that distinguishes a primary species concept that tells us something about species ontology in a biological way (what species taxa are) from secondary species criteria that tell us how to identify the entities defined by the primary concept. This has been suggested independently by Richard Mayden and Kevin de Queiroz. Mayden considers the Evolutionary Species Concept as the primary concept, de Queiroz the General Lineage (or Unified) Species Concept, but these concepts are both very similar and perhaps identical for most intents and purposes. They emphasize that all approaches to species agree that species are separately or independently evolving population-level lineages. All other species concepts (or criteria on this view) serve to identify these independent lineages by showing, for example, that they are reproductively isolated (Biological Species Concept), inhabit different ecological niches (Ecological Species Concept), are reciprocally monophyletic or diagnosably distinct (different versions of the Phylogenetic

Species Concept), etc. An important aspect of this view is that it entails and acknowledges that all species concepts are based on biological realities. This means that these concepts may be limited in their applicability, perhaps prone to recognize entities that others consider trivial and not worthy of bearing a species name, but they cannot be wrong! While this solves the grouping problem, at least in theory, the fractal nature of the Tree of Life, with lineages within lineages and so forth, makes completely non-arbitrary species delimitation and ranking (defining the species rank in the hierarchy of our classifications) much more problematic, indeed in all likelihood impossible.

Nature is particularly messy in the prokaryotic world where horizontal/lateral gene flow is so rampant that a core genome shared by all strains of a species is distinguished from a pan-genome that also comprises those genes that are found in some but not all strains of a species and delineates the gene pool within which horizontal gene flow involving the species occurs. Prokaryotic classifications may never come close to bridging the gap between T and E species.

Fuzzy boundaries at and around the species level make a completely non-arbitrary delimitation of species impossible. The introduction of additional categories like superspecies and subspecies increases the available arsenal to tackle this grey area, but it does not solve the problem because these categories face the same or even more problems about their objectivity. A truly objective classification based on independent population-level lineages would have to assign species status to every single allopatric deme or even every single allopatric pair of male and female individuals, including captive breeding populations and individuals dispersed by human transportation (like mosquitos on an airplane). This is of course neither feasible nor desirable, and even such an approach would suffer from grey areas such as the one arising from the fact that even allopatry, like so many other biological phenomena, is a continuum. The only solution to this is that species can only be delimited retrospectively, when it becomes clear or at least very probable that splits are permanent and that the two or more population-level lineages really evolve independently and have different historical fates. The famous tokogeny/phylogeny divide therefore cannot be taken literally at any one time but has to be inferred in hindsight. From this it follows that many closely related population-level lineages can be assigned to either one or several species, without the possibility of deciding either way at the moment.

While unbranched lineages through time cannot and should not be split up into artificial “chronospecies”, the situation at any one horizontal time plane (i.e. as a cross-section through the Tree of Life) is less clear-cut. Here, there is no such objective decision how not to delimit species, and ultimately, we will have to decide on some standardized criterion about how inclusive species should be. This will have to include some level of maximum intraspecific divergence and therefore ultimately a threshold of similarity that is required for two organisms to be conspecific. While such an approach is possible and would, ideally, guarantee repeatability of species delimitation, it will not be completely objective. Objective taxonomic boundaries are wishful thinking in a world where the real underlying biological boundaries are inherently vague.

As a consequence, it is unclear in how far different species taxa share more than their being real in the sense of being historical entities and their being classified at the same rank (that of the species category). It is most doubtful when it comes to sexual vs asexual organisms because the latter do not even form the same kind of population-level lineages as the former. However, it is also at least questionable if species are really comparable within sexual and asexual taxa. This holds regardless of whether one rejects species pluralism and only accepts one type of species that is delimited, for example, based on reproductive isolation (*or* ecological niches *or* monophyly *or* diagnosability, etc.). Whether there is really an objective level called species in our classifications across the Tree of Life or at least across parts of it and whether we can realistically hope to recognize it if it exists are unanswered questions. Yet the practical relevance of the answers to these questions can hardly be overestimated. Populations that are acknowledged taxonomically as species or subspecies have a different legal status when it comes to protection and management. Even more relevant from a scientific point of view is that species are the most important currency in many disciplines of ecology and evolutionary biology. Biodiversity is often quantified by means of species richness—resulting in conclusions on conservation priority areas; measures of evolutionary diversification and success; identification, spatiotemporal delineation, quantification of extinction events, etc. Depending on where species boundaries are drawn, the resulting species will be more or less widespread, more or less ecologically plastic and more or less diverse genotypically and phenotypically. Any inferences and conclusions drawn from such datasets critically hinge on species taxa being the same kind of thing. If they are not, and we are far from sure to know if they are, many of our ecological and evolutionary studies will be flawed or at least biased. If this is true, biologists will have to get used to the fact that species are not fundamentally different from higher categories (“families”, “orders”, “classes”, etc.) in this regard, and they should be very careful not to compare apples with oranges.

Glossary[1]

Allele Different forms or variants of a gene or, more generally, locus. Blue and brown, for instance, are alleles of the eye colour gene.

Allopatry Spatial separation (as opposed to **Sympatry**); allopatric populations occur in separated, disjunct areas. Organisms occurring in the same larger area but in different habitats are said to be allotopic (microallopatric, as opposed to syntopic = microsympatric). See also **Parapatry** and **Sympatry**.

Allospecies See **Superspecies**.

Anagenesis Evolutionary changes within a single line of descent through time (i.e. without lineage splitting).

Anaphylum A group that shows both "network gain(s)" and "network loss(es)"; i.e. it contains the descendant(s) of one or more hybridization events between one of the in-group members with an organism outside the group ("network gain") but not those of one or more other such hybridization events ("network loss"). Cf **Epiphylum** and **Periphylum**.

Apomorphy A derived character state (i.e. an evolutionary novelty). Note that this is a relative term: three auditory ossicles are an apomorphy for mammals, but a **Plesiomorphy** for primates; i.e. the trait "three auditory ossicles" is evidence for the monophyly of mammals but not for that of primates.

Assortative mating Non-random mating such that individuals more similar than average to one another have a higher mating probability. See also **Disassortative mating**.

Biodiversity hotspot In a wider sense, any area with high biodiversity; in a strict sense, those areas that harbour at least 1500 endemic (= 0.5 % of all known) vascular plant species and that have lost 70 % or more of their primary vegetation. These two criteria, irreplaceability and vulnerability, are used to prioritize conservation areas. At present, 36 biodiversity hotspots s. str. are known.

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[1] Some of the succinct formulations are modelled on those in Lincoln et al. (1998). Definitions of the various species concepts are not included here; instead, see Chap. 4.

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Chronospecies Species along a single phyletic lineage that are distinguished morphologically from earlier and later forms. Often used for convenience in palaeontology, but it is an arbitrary subdivision of a continuous lineage which is why the existence of chronospecies is rejected by many.

Class A spatiotemporally unrestricted group that is defined by essential (= necessary and sufficient) properties such that all and only those particulars that exhibit these properties are elements of that class. This common definition is also called a monothetic class, while a polythetic or cluster class is different in that it is only loosely essentialist: elements need not exhibit all defining properties but only a certain minimum number of them, i.e. no single property is necessary or sufficient. The term "set" is sometimes used synonymously with class, but often the name set is reserved for **extensionally defined** groups (as opposed to **intensionally defined** classes).

Coalescent (theory) A retrospective mathematical and probabilistic population genetic theory of the evolutionary history of alleles in a population going back to the common ancestry ("coalescence") of alleles in the most recent common ancestor. It allows for inferences on demographic history and genetic diversity through time and is also relevant to phylogenetic inference as gene trees may differ from the underlying organismal relationships.

Cryptic species Species that are so far undetected because they are (erroneously) thought to be part of another, very similar species.

Definition see **Extensional definition**, **Intensional definition** and **Ostensive definition**.

Diachronic species Species through time. This term highlights the vertical (time) dimension of species, that they have a temporal extension and do not just exist at one time horizon. The diachronic dimension of species emphasizes their historical individuality (similar to that of supraspecific monophyla). See also **Synchronic species**.

Diagnosability, qualitative Diagnosability due to fixed difference(s) between two or more groups, i.e. all individuals of one group differ in this trait from all individuals of the other group(s). Each single individual can be unambiguously assigned to its population on the basis of its characters (the fixed ones) alone. Qualitative diagnosability is therefore due to a difference in kind. See also **Diagnosability, quantitative**.

Diagnosability, quantitative (or statistical) Diagnosability due to population-level statistical differences between two or more groups; diagnosability is not based on fixed differences, individuals can be assigned unambiguously to their population, but only in a statistical approach including the population data. Quantitative diagnosability is thus based on a difference in degree. See also **Diagnosability, qualitative**.

Diairesis (Greek for "division") Plato's method of definition in which the final definition of a term is reached through repeated dichotomous division of more inclusive terms (a method mirrored in modern biological identification keys for species).

Disassortative mating Non-random mating such that individuals more dissimilar than average to one another have a higher mating probability. See also **Assortative mating**.

Epiphylum A monophyletic group that also contains the descendant(s) of one or more hybridization events between one of the in-group members and an organism outside the group ("network gain"). Cf **Anaphylum** and **Periphylum**.

Essentialism The view that an entity has an essence, i.e. one or more necessary and sufficient characters. Entities with essences are classes (or **Natural kinds**): the class of red triangles has triangular shape and red colour as necessary and sufficient characters, i.e. all elements of that class are red and triangular, and all red and triangular objects are elements of that class.

Essentialism Story (also called Received View) The historical misconception that notions about species were locked in **Essentialism** for more than 2000 years, going back to Platonic idealism and Aristotelian logic and being overcome only by Darwin in the nineteenth century. However, it is becoming increasingly clear that species notions before Darwin were rarely really essentialist (including Linnaeus!) but rather diverse and usually contained an element of descent and generation of like kind (see **Generative conception of species**).

Evolutionary species (E species) The species as the unit of evolutionary processes (as opposed to the unit of classification). (The term is also used with a different meaning: as a species according to the Evolutionary Species Concept.) See also **Taxonomic species**.

Exclusivity A group is called exclusive if all its members are more closely related to one another than to any organism outside the group. In a strictly divergent (splitting) phylogeny or genealogy, monophyletic groups (and only monophyletic groups) will be exclusive. However, in the case of reticulation (through hybridization), exclusivity and monophyly are not identical if monophyla are defined as groups comprising an ancestor and all and only its descendants. There are other definitions of monophyly, though (including one identical to the exclusivity definition here). In the Genealogical Species Concept, exclusivity is not defined by means of recency of common organismic ancestor but in terms of gene coalescence such that a group of organisms is exclusive if their genes coalesce more recently within the group than with any organism outside the group.

Extensional definition Defining an entity by giving its extension, i.e. a list of all objects that belong to this entity. An extensional definition of "bachelor" would be a list of all unmarried men in the world. See also **Intensional definition** and **Ostensive definition**.

Family resemblance (translated from the German *Familienähnlichkeit*) A cluster class concept in Ludwig Wittgenstein's philosophy where the members of a **Class** (Wittgenstein's best-known example is games) are connected by a number of overlapping similarities, none of which, however, is common to all members.

Fixism See **Species fixism**.

Founder effect The presence in the founding members of a population of only a fraction of the genetic diversity of the parental or ancestral population. The founder effect is a sampling effect (see **Genetic drift**).

Generative conception of species According to John S. Wilkins, the predominant notion of species since the Epicureans in ancient Greece. He calls it the "marriage of reproduction, or generation, with form", and it holds that there has always been an element of descent or genealogy in species notions, coupled with the idea of a generative power that makes offspring resemble their parents.

Genetic drift Random changes in a gene pool through time due to sampling effects in a population of finite size.

Haldane's rule Empirical rule saying that if there is a bias towards one sex when it comes to sterility or inviability in hybrids, it will be the heterogametic sex (i.e. the one with two different sex chromosomes, e.g. XY males in mammals and ZW females in birds). Haldane's original formulation reads "When in the F_1 offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous [= heterogametic] sex" (Haldane 1922, p. 101).

Hennigian Convention The view that upon the splitting of a lineage in a speciation event, the ancestral species must be considered extinct, i.e. there is no budding off of a daughter species from a surviving ancestral species, but always the production of two new daughter species that must be assigned new binomial names. It is contentious, though, whether this is only a taxonomic necessity ("taxonomic extinction" of the ancestral species) or really means that the ancestral lineage ceases to exist.

Hologenetic relationships Willi Hennig's term (following Walter Zimmermann) for the totality of ontogenetic, **tokogenetic** and **phylogenetic** relationships.

Homeostatic property cluster A cluster class or cluster kind concept according to which all members of the class have a number of co-occurring similarities no single of which is necessary and whose probability of co-occurrence is higher than chance because of homeostatic mechanisms acting on all members of the class (in the case of organisms, e.g. interbreeding, developmental constraints or similar selection pressures).

Homology The presence of a structure in two or more organisms due to common ancestry (regardless of how different the structures are in the descendants).

Homoplasy Structural resemblance in two or more organisms that is not due to common ancestry (homology) but due to parallel or convergent evolution (analogy).

Horizontal gene transfer See **Lateral gene transfer**.

Hybrid zone The area of overlap between adjacent populations, subspecies, species, etc. where interbreeding occurs.

Hybridization The mating of two individuals of different genetic compositions. The term can be used on various levels, depending on the issue at hand: hybridization between species, between subspecies and ESUs, between populations that are rather similar genetically, etc. Hybridization only refers to the production of hybrid offspring; it does not necessarily include the successful spread of genetic material in a gene pool, which is called introgressive hybridization (see **Introgression**).

Identical by descent (IBD) Homologous allelic identity. Two alleles are said to be identical by descent if their identity is due to common ancestry (i.e. both identical copies ultimately go back to the same ancestral individual). See also **Identical by state**. Caution: IBD can also refer to **Isolation by distance**.

Identical by state (IBS) Homoplasious allelic identity. Two alleles are said to be identical by state if their identity is due to two independent mutational events and not due to common ancestry. See also **Identical by descent**.

Individual Any historical, i.e. spatiotemporally limited, entity. This can be an inanimate object like a stone or table, a cell, a single organism or groups of organisms like populations, royal dynasties or, as most would agree, also species.

Infima species In a logical division or classification, that species (in the logical sense of the word) that is not a genus to a lower species; the lowest level in a logical classification. See also **Summum genus** and **Porphyrian tree**.

Integrative taxonomy A taxonomic approach making use of all data and methods available in systematic biology.

Intensional definition A definition based on specifying the necessary and sufficient (i.e. essential) properties for belonging to the defined entity. An intensional definition of the term “bachelor” would be “unmarried man”, the two essential properties are being unmarried and being an adult male human. See also **Extensional definition** and **Ostensive definition**.

Introgression The successful spread of genetic material of one population, subspecies, species, etc. into the gene pool of another through hybridization (and backcrossing).

Isolation by distance (IBD) The pattern in which genetic or evolutionary distance between populations increases with geographic distance due to increasingly limited gene flow. Caution: IBD can also refer to **Identical by descent**.

Lateral gene transfer (also called horizontal gene transfer) Transfer of genetic material between organisms by mechanisms other than reproduction, e.g. through bacterial conjugation, the introduction and incorporation of foreign genetic material through the cell membrane (transformation) or virally mediated introduction of genetic material in bacteria (transduction). The term lateral or horizontal distinguishes this kind of transfer from the vertical transfer of genetic material from the parental generation to the offspring.

Metaspecies A (not very widespread) term with at least two different meanings: (1) a non-monophyletic ancestral or stem group at the same hierarchical level as species. The motivation for this usage is to distinguish these entities from species if one holds that species must be monophyletic. Since ancestral species are by definition paraphyletic, they are given an alternative name. If one discards the monophyly criterion for species, there is no need for this term. (2) Species whose phylogenetic status has not been resolved, i.e. for which it is not (yet) known whether they are monophyletic or not. Metaspecies in this second meaning have been suggested to be marked with an asterisk to distinguish them from species whose monophyly has been confirmed. Again, this presupposes that species should be monophyletic, which is contentious.

Modern (Evolutionary) Synthesis The time from around 1920 to 1950 when the major publications leading to the Synthetic Theory of Evolution were published that combined modern genetic knowledge with the selectionist views of "classical" biologists and rejected Lamarckism, orthogenesis (the idea that organisms have an inherent driving force that makes them evolve along predetermined evolutionary trajectories), saltationism and related concepts.

Monophylum Usually defined as a taxon whose members all have a common ancestor and that comprises this ancestor and all and only the descendants of it; in short, an ancestor and all and only its descendants. A hypothesis of monophyly is founded on the existence of shared derived traits (apomorphies). Examples: Mammalia, Arthropoda and Metazoa. See also **Paraphylum** and **Polyphylum**.

Monotypic species A taxonomically "homogeneous" species, i.e. one that does not comprise different subspecies. Opposite: **Polytypic species**.

Natural kind Classes of objects that are believed to correspond to groupings that reflect the structure of the natural world (i.e. have extramental reality) rather than only mental constructs of humans. The prime examples of natural kinds are chemical elements: they have essential properties (atomic number) and are thus classes, but they are also believed to be real in an objective way because what unites them is not the human mind but natural causes and laws.

Ostensive definition "Definition by pointing", i.e. by pointing out examples. Naming is an ostensive definition because individuals (as opposed to universals) have proper names and cannot be defined by giving essential properties. See also **Extensional definition** and **Intensional definition**.

Pan-genome In microbiology the totality of genes found in a bacterial species, i.e. the combined gene pool of all genes found in all members of a species (core genome) and of all genes found only in some but not all members of the species (dispensable genome). Genes of the dispensable genome can be introduced by **Lateral gene transfer**.

Parapatry Occurrence in two contiguous but nonoverlapping areas. See also **Allopatry** and **Sympatry**.

Paraphylum A taxon whose members all have a common ancestor but which does not comprise all the descendants of that ancestor. Members of a paraphyletic taxon do not share apomorphies (synapomorphies) but are grouped together based on shared plesiomorphies (symplesiomorphies). The most famous example of a paraphylum is reptiles which share a common ancestor with birds and are thus not monophyletic but which are often nonetheless classified as a taxon Reptilia. See also **Monophylum** and **Polyphylum**.

Paraspecies A term denoting (1) an asexual taxon analogous to the species in sexual organisms or (2) a paraphyletic species.

Pattern cladism/cladistics Also called transformed cladism/cladistics. A version of cladistics that aims at a theory-free classification based on character distribution ("pattern") alone, without reference to evolutionary theory and the processes that gave rise to the observed pattern. Instead of trees or cladograms, relationships are often depicted as sets within sets ("boxes within boxes"). Evolution is not denied, just divorced from classification and systematics. The mode of inference is the same as within classical or process cladistics, but the underlying theory is different. Cf **Process cladism/cladistics**.

Periphylum A group that is not monophyletic (anymore) because it does not contain the descendant(s) of one or more hybridization events between one of the in-group members and an organism outside the group ("network loss"). Cf **Anaphylum** and **Epiphylum**.

Phyletic evolution See **Anagenesis**.

Phyletic speciation See **Chronospecies**.

PhyloCode (International Code of Phylogenetic Nomenclature) An alternative nomenclatural code for taxonomy that, unlike the present rank-based codes, names taxa (clades) through explicit reference to phylogeny.

Phylogenetic diversity In its broad sense, a biodiversity measure that includes a quantification of how different species are from one another (e.g. based on branch lengths along an evolutionary tree); in a narrower sense, the particular approach making use of phylogenetic diversity introduced by Faith (1992).

Phylogenetic relationships Evolutionary relationships of populations, species and supraspecific taxa or, more generally, of entities *within* which **Tokogenetic relationships** exist but *among* which there are none. See also **Hologenetic relationships**.

Plesiomorphy An ancestral ("primitive") character state. This term is a relative one—a character state can only be plesiomorphic compared to an evolutionarily younger **apomorphic** ("derived") state.

Polymorphism The presence of more than one character state or allele in a population or gene pool.

Polyphylum A taxon that combines two or more non-closely related groups based on homoplasy rather than homology. For example, birds and mammals have been combined into Haemothermia based on the fact that both are homeothermic and have a four-chambered heart with complete separation of oxygenated and deoxygenated blood (Gardiner 1982), but it is now general consensus (in fact, it is beyond reasonable doubt) that these conditions evolved independently in the two lineages. See also **Monophylum** and **Paraphylum**.

Polytypic species A species comprised of two or more differentiated subgroups. Most often used with regard to the subspecies concept and denoting species that comprise at least two subspecies. The opposite is the **Monotypic species**. Polytypic species are particularly often found under the Biological Species Concept, and the concept is most often criticized by adherents of Phylogenetic Species Concepts.

Porphyrian tree (Arbor Porphyriana) A tree-like graphical representation of the top-down classification of Platonic–Aristotelian logic. It begins with the highest level, the **Summum genus**, and, based on increasingly specific differences (*differentiae*), subdivides entities until the lowest level, the **Infima species**, is reached.

Process cladism/cladistics The classical cladistics school founded by Willi Hennig (*Phylogenetic Systematics*, 1966) that is explicitly rooted in evolutionary theory and groupings based on recency of common ancestry. Baum and Donoghue (1995) call it "evolutionary phylogenetics". Cf **Pattern cladism/cladistics**.

Reinforcement (also called Wallace effect) Selection against hybrids in areas of sympatry of two populations such that divergence of the two populations is accelerated (reinforced).

Ring species A series of adjacent populations that curves round on itself in such a way that the populations at the extremes overlap but are unable to interbreed successfully while at the same time being connected by gene flow via the populations between them.

Selection Differential reproductive success that is non-random (i.e. due to an adaptive advantage).

Semaphoront "Character bearer": Willi Hennig's term for the basic unit of phylogenetic analysis. The semaphoront is an individual organism during a (theoretically infinitesimally) small period of its life such that the characters under study can be regarded as constant (not changing either ontogenetically or phylogenetically).

Semispecies See **Superspecies**.

Set See explanation under **Class**.

Sibling species Two or more closely related and morphologically (almost) indistinguishable species that are nonetheless reproductively isolated.

Speciation The origination of one or more new species; more generally, the ultimately irreversible process of divergence between population lineages.

Speciation genes There are several definitions of speciation genes, most or all of which include causing an increase in reproductive isolation or a decrease in gene flow among populations. A recent and general one is "those genes whose divergence made a significant contribution to the evolution of reproductive isolation between populations" (Nosil and Schluter 2011, p. 160).

Species (category) The level or rank of species in a hierarchical classification; the class of all **Species taxa**.

Species (taxon) A single lineage in the Tree of Life that is considered to be at species level, for example, *Homo sapiens* or the tiger (*Panthera tigris*). Humans and tigers can be real regardless of whether they are comparable enough to be assigned the same rank (that of the **Species category**).

Species concept The definition of the **Species category** (ideally one that applies to all groups of organisms). Some species concepts are true definitions of what the class of **Species taxa** is (primary or ontological concepts); others are rather identification criteria to discover species taxa (secondary or operational concepts).

Species fixism The view that species do not evolve into other species or are descended from them. Basically the opposite of Darwin's "descent with modification", although some change (within species limits) is often allowed for.

Species monism The view that there is a single best definition of the **Species category**, i.e. a single species concept that applies to all species taxa regardless of circumstances and taxonomic group. See also **Species pluralism**.

Species nominalism The view that species only exist in human minds, but have no reality independent of the human intellect. There are two very different kinds of species nominalism that must not be confused: nominalism with respect to the **Species category** and nominalism with regard to **Species taxa**. Species category nominalism does not deny the reality of species taxa such as lion, tiger or *Homo sapiens*, but rejects the idea that these taxa are directly comparable entities, i.e. that there is something like the species level that deserves a name or rank. Species taxon nominalism is more extreme in that it also holds that what we unite into species are arbitrary groupings within a continuum of living beings. See also **Species realism**.

Species pluralism The view that there is no single correct definition of the **Species category** but that different definitions are appropriate or even necessary in different circumstances or for different taxa, resulting in *different kinds of species* (such as, e.g. sexual species and asexual species, interbreeding species, ecological species, monophyletic species, etc.). If this is true, the term species denotes very different entities and cannot be used without further specification. In particular, analyses based on species counts (e.g. for quantifying biodiversity) may be seriously flawed. See also **Species monism**.

Species realism The view that species taxa (**Species taxon** realism) or the species category (**Species category** realism) have reality also outside the human mind. See also **Species nominalism**.

Species richness The number of species in a given area or group of organisms.

Species selection Selection not on the level of the individual (via reproductive success and survival against death) but among the species as a whole (via differential rates of speciation and survival against extinction). Species selection implies that selection acts on species-intrinsic properties (not properties of individual organisms); such species-intrinsic properties might be population structure (which may or may not favour divergence and ultimately speciation) or geographic distribution (which might affect the probability of extinction). Whether species selection really occurs and, if it does, whether it is an important factor in evolution is highly contentious.

Summum genus In a logical division or classification that genus (in the logical sense of the word) that is not a species to a higher genus; the highest level in a logical classification. See also **Infima species** and **Porphyrian tree**.

Superspecies A concept going back to the German *Artenkreis* (circle of species). It usually denotes a monophyletic group of closely related and similar species. Member species of a superspecies are allospecies and semispecies. The exact meaning of these terms has changed through time (see Sect. 5.9), but in the most widely used present framework, implemented, for example, in the taxonomic guidelines of the British Ornithologists' Union, allospecies are allopatric species within a superspecies, whereas semispecies are connected by a stable hybrid zone.

Sympatry Occurrence in the same area. On a finer scale, when organisms occur in the same habitat, the term syntopy (microsympatry) is often used; organisms occurring in the same area but in different habitats are said to be allotopic (microallopatric). See also **Allopatry** and **Parapatry**.

Synchronic species Species at one time horizon, not considering the temporal extension of species. The criterion of interbreeding (as in the Biological Species Concept) is only applicable synchronically. The synchronic aspect of species emphasizes their individuality with respect to cohesion and interactions; in other words, these conspecific organisms behave as a unit in some way, for example, through reproduction and gene flow or by evolving as a unit in response to common selection pressures, etc. See also **Diachronic species**.

Taxonomic inflation The increase in species number due to a shift from one species concept to another that is considered to assign species status to smaller population-level lineages that are considered insignificant by many. Most often discussed in the context of the diagnosability version of the Phylogenetic Species Concept.

Taxonomic species (T species) The species as the unit of classification (as opposed to the unit of evolutionary processes). See also **Evolutionary species**.

Tokogenetic relationships Genetic relationships between individual organisms arising through reproduction. Usually the term tokogeny is applied to biparental reproduction, but some authors include asexual or uniparental reproduction in the concept so that tokogenetic relationships also exist among uniparental organisms. In the latter sense, it does not entail reticulation; in the former (and usual) sense it does. See **Hologenetic relationships** and **Phylogenetic relationships**.

Transformed cladism/cladistics See **Pattern cladism/cladistics**.

Wallace effect See **Reinforcement**.

References

As has often been stated, the literature about species concepts and the species problem is vast. The references in this list are only a selection of the available publications. Three monographs that I found very useful and informative are Stamos (2003), Wilkins (2009a) and Richards (2010). Richards also briefly summarizes his views in Richards (2013). All three books are rather theoretical and written from a philosophical and/or historical perspective. Richards (2010) combines history with theory; the focus of Wilkins (2009a), while also discussing theoretical aspects, is on the history of notions about species. Wilkins (2009b) is a sourcebook compiling all relevant authors and excerpts from their works from Plato and Aristotle to the twenty-first century. It is an invaluable compilation for anyone interested in the original publications and not only in secondary sources. The most detailed account of the ontology or metaphysics of species, whether they are classes, individuals or something else altogether (relations as the author holds), is the book by Stamos (2003; a quite extensive review of that book is given by LaPorte 2006). It also includes a chapter on species nominalism, historical sections and quite some discussion on a variety of modern species concepts. It contains an in-depth discussion of Darwin's views on species—yet much more detailedly set out in Stamos (2007)—, but the pre-Darwinian historical account is basically one embracing the "Essentialism Story" (Stamos is one of the few who at least partly still defends this view; see Stamos 2005). Taken together, this book may be the single most detailed discussion of the species problem, but it is first and foremost a philosophical book (and quite detailed and technical at that), so perhaps it is not the first choice for biologists. However, as announced by the author, it does take biological issues seriously, and the theoretical aspects of evolutionary biology that form the scientific backbone of the discussion are well worked out. Obviously, the author has read extensively on these topics. When it comes to more practical or methodological issues, this is sometimes different: for example, biologists will be surprised to read that DNA–DNA hybridization is praised as one of "the most common and powerful techniques" (p. 300, footnote 11) in molecular phylogenetics, although it had long been outdated even by the time the book was published.

F.E. Zachos, *Species Concepts in Biology*, DOI 10.1007/978-3-319-44966-1

It should be emphasized, however, that it is the theoretical biological issues that matter in the context of this book, and here the author is very knowledgeable.

Ereshefsky (2001) is also worth mentioning. Although dealing with taxonomy in general, and particularly the Linnaean version of it and its shortcomings, the book contains many relevant sections on species. The little history of species concepts that is in it perpetuates the "Essentialism Story", but that does not at all diminish the other parts that contain nice overviews and discussions about, among other things, the species-as-individuals concept and species pluralism vs species monism. The book by Hey (2001a) offers an interesting discussion about the cognitive aspects and causes of the species problem, a "Kantian" explanation (without mentioning Kant, incidentally) how our minds and our language introduce a bias towards perceiving species as classes despite their being historical entities or individuals. I think there are some genuine insights here, and the book also discusses practical consequences (e.g. when it comes to species counts), but it is also a bit lengthy. One reviewer bemoaned "too many words chasing too few ideas" (Brookfield 2002, p. 108), but the ideas are still worth pondering, I think. Therefore, for most purposes it may suffice to read a short review by the author on the same topic (Hey 2001b), which is something like the book in a nutshell.

And there is, of course, *Metaphysics and the Origin of Species* by Ghiselin (1997), the father of the species-as-individuals thesis. This book, whose title shows the author's affinity towards views of the Modern Synthesis and the Biological Species Concept (compare the title to those of Dobzhansky 1937 and Mayr 1942[2]), is wider in scope than other books on the issue of biological species. Although it contains sections on various species concepts, it is not simply a book on species concepts at all, but rather a long and detailed explication of the individuality thesis and the concept of individuality in general (as opposed to universals) and its biological and philosophical corollaries. As such it is a scholarly volume and at times brilliantly written with a very useful and elegant appendix (a collection of aphorisms and definitions), presented by perhaps the most philosophical of all biologists dealing with this topic. It is also far less neutral in style than other books; in fact, Ghiselin can be quite provocative and is at times rather dismissive and offensive when discussing what he thinks is bad metaphysics. A critical, sometimes ironical and very elegantly written review of this book is presented by Ruse (1998).

There are a number of edited volumes that are important. The book by Ereshefsky (1992) is a collection of classical papers on the species problem, including Ghiselin's (1974a) seminal paper on the individuality thesis, Hull's classical papers from 1965 on the alleged essentialism in pre-Darwinian taxonomy and a number of first or very relevant publications of several species concepts (Ecological, Van Valen 1976; Evolutionary, Wiley 1978; Phylogenetic, Cracraft

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[2] Ghiselin (1997, p. 16) explains the allusion of the title of his book to those of the others by saying that his "aims at a metaphysical synthesis that continues the tradition of its justly illustrious predecessors".

1983; Recognition, Paterson 1985; Cohesion, Templeton 1989). The book by Wilson (1999b) mainly contains philosophical chapters, among others Boyd's paper on homeostatic property clusters. Claridge et al. (1997) present contributions on species concepts in theory and practice for different taxonomic groups, and it contains some general theoretical chapters as well, among them Mayden's paper on the hierarchy of species concepts, which is arguably one of the most important papers on the topic within the last 20 or so years. The book by Wheeler and Meier (2000) is structured like a scientific debate. It covers five of the most influential species concepts (Biological, Evolutionary, Hennigian and the diagnosability and monophyly versions of the Phylogenetic Species Concept). Each author or author team first introduces their concept (position papers), then criticizes their competitors (critique papers) and finally responds to these criticisms of their own concept (reply papers). This structure makes it a unique comparative overview of the five concepts covered. It also contains a very readable introductory chapter by Joel Cracraft. Avise (2000b) provides a somewhat satirical review (garnished with quotations from "Alice in Wonderland"), particularly criticizing Phylogenetic Species Concepts. The most recent edited volume is by Pavlinov (2013). It combines articles on various aspects of the species problem including a summary on species delimitation methods by Camargo and Sites and chapters by Richards, Mayden and Stamos in which they summarize and update their views from Richards (2010), Mayden (1997) and Stamos (2007).

There are also three review articles or chapters that can be recommended as introductory reading, all of them encyclopaedia entries: Mallet (2001a), Ghiselin (2001) and Ereshefsky (2010a). The first of these three is the least philosophical one, Ghiselin covers both biology and philosophy, and Ereshefsky writes from a primarily philosophical perspective. The combination of these three is, in my view, the ideal starting point for a deeper understanding of the species problem. It should be mentioned, however, that the few historical remarks in Ghiselin (2001) and Ereshefsky (2010a) perpetuate the misconception of what is known as the Essentialism Story (see Sect. 2.1). Since history, however, is not the main topic of their reviews, this does not diminish the value of the rest of their papers. The edited volume by Keller and Lloyd (1992) also contains three entries on species: Stevens (1992) on (some aspects of) the history of the term and Dupré (1992) and Williams (1992) on theoretical issues including the individuality thesis and species as taxonomic and evolutionary units. While these short articles of course do not include the more recent literature and insights, they are nonetheless concise and readable starting points as well. The same applies to the species concepts chapter in Ward (not Quentin) Wheeler's (2012) book on systematics. It, too, perpetuates the simplistic view of the Essentialism Story but also gives a short overview of recent species concepts and, as a bonus, contains many photographs of various scientists who have introduced or popularized these concepts. Finally, the nice article by Minelli (2015) includes short discussions and definitions of species concepts and related topics, with nice examples from the literature and a good reference list.

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