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.

Vienna, Austria Frank E. Zachos
04 July 2016

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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

[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.

[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

[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.

[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

[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

[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

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.

[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