3 On the nature of the species problem and the four meanings of ‘species’

Abstract

Present-day thought on the notion of species is troubled by a mistaken understanding of the nature of the issue: while the species problem is commonly understood as concerning the epistemology and ontology of one single scientific concept, I argue that in fact there are multiple distinct concepts at stake. An approach to the species problem is presented that interprets the term ‘species’ as the placeholder for four distinct scientific concepts, each having its own role in biological theory, and an explication is given of the concepts involved. To illustrate how these concepts are commonly conflated, two widely accepted ideas on species are criticized: species individualism and species pluralism. I argue that by failing to distinguish between the four concepts and their particular roles in contemporary biological theory, these ideas stand in the way of a final resolution of the species problem.

This chapter has been published as:
Reydon, T. A. C. (2005). On the nature of the species problem and the four meanings of ‘species’. *Studies in History and Philosophy of Biological and Biomedical Sciences* 36: 135-158.

> *"There is already too much literature on the "species problem" (…) Anyone who wades through that literature must surely be reminded of the fable of the blind men and the elephant, and must come to realize that much of the so-called problem results from the fact that there isn't just* one *elephant and that they aren't all even* elephants *(…)" (Winston, 1999: 43-44)*

3.1. Introduction

The current state of affairs regarding the species problem is intriguing. As can be seen from recent exponents of the debate, such as Claridge *et al.* (1997), Howard & Berlocher (1998), Wilson (1999), Wheeler & Meier (2000) and (to a lesser extent) Stamos (2003), the debate on the correct definition of the notion of species continues without much promise of imminent resolution. In stark contrast, however, the view has emerged among some biologists and philosophers of biology that the species problem is all but solved. Assertions like the following are exemplary:

> "(…) the species problem has, for the most part, already been solved. Despite the considerable diversity among contemporary views on species, all are encompassed by a single, general concept that equates species with segments of population-level lineages." (De Queiroz, 1999: 49; cf. De Queiroz, 1998: 57-60).

The present chapter is motivated by the view that assertions like the above are mistaken and sketch an unduly optimistic picture of the present-day state of affairs regarding the species problem. My aim is to show why this optimistic view of the problem is indeed mistaken. The main reason, I shall argue, is the following: whereas the species problem is commonly understood as concerning one single scientific concept, in fact multiple distinct and independent concepts are at stake.

Several authors have earlier made the observation that the term 'species' is used to denote a number of different concepts. By far most of these authors, however, either have made the observation only in passing (e.g., Williams, 1992; Kornet, 1993) or have taken it as a starting point to defend some form of species pluralism, that is, the view that the concepts at stake are not independent but constitute subconcepts of some overarching concept of species (e.g., Kitcher, 1984a; Ereshefsky, 1992). So far, none have drawn the consequence that the concepts at stake constitute wholly independent concepts that possess different ontological status as well as perform different roles in biological investigation, and consequently cannot be considered as ultimately falling under one single overarching concept of species.[1] That is, that 'species' is a homonymic term denoting multiple independent concepts, not a pluralistic term denoting multiple closely or even distantly connected concepts.

I argue for this view of the species problem by means of an epistemological and ontological analysis of the term 'species' (Section 3.2) and a consideration of two important ideas that have been advanced with respect to the species question (Section 3.3). In Section 3.2.1, I consider the various epistemic roles that the term 'species' performs in biological theory, in relation to the research questions that the various biological disciplines aim to answer. These roles often impose incompatible requirements on the definitions of the term for different contexts of research. If the term 'species' is taken as denoting one single, undifferentiated scientific concept, these criteria cannot all be met. This problem does not occur, I argue, when the term 'species' is interpreted as the placeholder for a number of distinct scientific concepts to which the various roles of 'species' can be attributed. In Section 3.2.2, I show that indeed a number of different concepts, with different ontological status, are denoted by the term 'species'. I distinguish four ontologies that the most important definitions of 'species' exemplify. Because these ontologies are profoundly different, they cannot be subsumed under a single overarching ontology and hence cannot be associated with one single scientific concept. This again shows that term 'species' should be understood as denoting multiple distinct scientific concepts (one for each ontology). In Section 3.2.3, it is shown how the various roles of the term 'species' relate to these four concepts.

The undue optimism regarding the species problem, referred to above, is fueled by a failure to distinguish between the various meanings of 'species'. To illustrate some of the problems that arise when conflating the various concepts at stake in the species

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[1] The radical pluralism defended by Dupré (1993) perhaps constitutes the only form of species pluralism that resembles the position defended here in some respects, because it allows species with different ontological status (including both classes and individuals). Nevertheless, Dupré (1993: 50-51) explicitly understands his position as a form of pluralism in that the different concepts at stake perform the same function in biological science (i.e., the function of units of classification; cf. Section 3.2.1) notwithstanding their ontological differences. In addition, in later work Dupré (1999: 18; 2001: 217) distanced himself from this radical pluralism and adopted a weaker and ontologically more homogeneous form of pluralism.

problem, in Section 3.3 I examine two ideas that strongly determine present-day thinking on the nature of species. One is the thesis that species are individuals rather than classes (Section 3.3.1), the other is species pluralism (Section 3.3.2). By propagating the mistaken understanding of the nature of the species problem as concerning a single scientific concept, these two ideas obstruct – rather than advance – the species problem's final resolution. This analysis of species individualism and species pluralism constitutes an indirect argument in support of the conclusion that the term 'species' is best understood as a homonymic term denoting multiple distinct concepts with distinct roles in biological theory[2] and that the species problem consequently is to be understood as a collection of distinct conceptual problems: there are as many 'species' problems as there are different concepts at stake.

3.2. Four 'species' concepts

3.2.1. Three epistemic roles of 'species'

During the development of biological science, the term 'species' has come to be used in three epistemic roles in biological investigation. At present the term still performs these roles. Although traditionally these roles have been – and still are – attributed to one undifferentiated concept of species, they constitute distinct roles that cannot all be performed by a single concept. The reason, as shown below, is that the demands a concept must meet in order to be able to play these various roles cannot all be met simultaneously. This indicates that 'species' is best seen as denoting multiple concepts that perform the epistemic roles of the term.

From Antiquity onward, the notion of species served as the basis for classifying organismal diversity in the context of uncovering and explaining the natural order in the living world. The term 'species' functioned in two roles that were understood as coinciding: as denoting the units of *classification*, i.e., the basic units in a general reference and information retrieval system that holds for the whole of biological science

[2] This position is different from Mayr's (1982: 253-254) and Mayden's (1997: 387-388, 1999: 103ff.) diagnosis that the term 'species' is a homonym because the term denotes both the species category and actual species. My concern here is not with this particular duality in the denotation of 'species', but with the multiple ontological categories denoted by the term.

and reflects the natural order of the living world, and the units of *generalization*, i.e., the fundamental groups of organisms over which explanatory and predictive generalizations can be formulated. Species were traditionally conceptualized as natural kinds in the Aristotelian, essentialist sense, that exist in nature independently from human classificatory purposes and that could feature in both scientific classification and generalization. By the end of the 19th century the – still undifferentiated – concept of species had gained firm ground as the central natural kind concept of biological science (McOuat, 2001: 617).

It is however far from self-evident that the aims of classification and generalization can be realized by means of a single concept (cf. Mayr, 1982: 148-149). For one, the classification of the whole of entities studied in a particular discipline into a storage-and-retrieval system requires that a concept be used that allows to divide up this whole into non-overlapping units and to attribute every entity to precisely one such unit. The making of explanatory and predictive generalizations over the member entities of the same group, in contrast, requires that a concept is used that allows to identify both the properties that all (or most) entities of the same group exhibit and the natural factors that underlie these properties.[3]

There is no a priori guarantee that the concept used to realize one of these aims in a particular scientific discipline will also be suitable to realize the other aim. In the physical sciences, it is found that both aims can be realized simultaneously by means of traditional essentialist natural kinds, such as the elements and isotopes in the Periodic System and the kinds of elementary particles. In the biological sciences, however, the acceptance of Darwinian evolution has rendered traditional essentialism untenable for classificatory purposes. Hull (1965: 321-326; 1987: 173-175), for example, famously argued that the binomial names of species taxa cannot be defined in terms of universal necessary and sufficient organismal properties and thus cannot feature in lawlike – that is: scientific – generalizations. Consequently, according to Hull, species cannot be conceived as the units of generalization but are to be seen as the units of classification. This move largely obscured the role of species as units of generalization in favor of their role as units of classification.[4] Nevertheless, the role of 'species' as denoting units of generalization has continued to be present in biology after the Darwinian revolution in

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[3] The issue of whether species can be conceptualized as units of generalization will be addressed in detail in Chapter 5.

[4] In a similar spirit, Griffiths (1974: 87) remarked that to understand biological systematics as delimiting units of generalization misses the point of systematics.

for instance Thompson's (1942) 'science of organismal form' (which continues to be an active field of research today; see Gould, 1976; Chaplain *et al*., 1999; Goodwin, 1999), the structuralist program in developmental biology (Goodwin, 1989; Webster & Goodwin, 1996; Goodwin, 1999) and the field of functional morphology.

With the establishment of the Modern Synthesis in the 1930s-1940s and its emphasis on evolutionary dynamics, the term 'species' adopted a third role as denoting the dynamic systems that are subject to evolutionary processes (Mayr, 1969: 26; 1982, pp. 296-297). The term 'species' did not undergo a complete shift of meaning in the synthesized disciplines but retained its classificatory meaning next to its new dynamic one because of the scientific prestige that it entailed: "The term itself brought with it much social capital. It referred to grounds." (McOuat, 2001: 640-641; see also Mayr, 1942: 111). These two roles however cannot be performed by the same entities, because units of classification are required to be stable and unchanging, whereas units of evolutionary dynamics are essentially subject to evolutionary change. Because of the requirement of stability, present-day biological classification (in the form of phylogenetic systematics) is founded upon evolutionary history (Hennig, 1966: 22-24; see also the historical discussion by Hull, 1988: 130ff.). The basic units of biological classification – species – then are conceptualized as parts of the tree of life that represents evolutionary history. Hull (1965: 1), for example, stated that "Species will be treated (…) from the point of view that classification must have some systematic relationship to phylogeny and that the unit of classification must be the unit of evolution", considering units of evolution to be lineages in the tree of life rather than dynamic entities that participate as wholes in evolutionary processes.

The three roles of 'species' distinguished above match the picture of biological science that was drawn by Mayr. According to Mayr, biology is divided into functional biology and evolutionary biology, "(…) two largely separate fields which differ greatly in method, *Fragestellung*, and basic concepts." (Mayr, 1961: 1501; cf. Mayr, 1982: 67-70). Evolutionary biology, in Mayr's view, encompasses both the study of evolutionary dynamics and systematic biology (Mayr, 1982, p. 70) and is thus concerned with the roles of 'species' as denoting units of evolutionary dynamics and units of classification. This dual role of 'species' within the context of evolutionary biology ignores the incompatibility of the criteria invoked in the two roles, but is widely acknowledged – see for example Dobzhansky (1970: 23 & 357-358); Ereshefsky (1992); Shaw (1998: 44-45); Dupré (2001) – and is usually attributed to an undifferentiated concept of species. Williams (1992), however, already noted that it may well be the case that in evolutionary biology 'species' possesses two distinct meanings, as denoting both the concept of T-species that functions as a classificatory concept in taxonomy and the concept of E-species that features as an entity-concept in evolutionary biology. Williams (1992: 320-321) pointed out that these two concepts have to satisfy different requirements, rendering it impossible to define 'species' in such a way that the concepts of T-species and E-species coincide:

> "(…) much of the problematic nature of the species concept may be due to its having been used to mean two intrinsically different things. (…) recognition of this fact may allow unproblematic definitions for each to be found." (Williams, 1992: 321).

The role of 'species' as denoting units of generalization features prominently (though not exclusively) in the field of functional biology, as distinguished by Mayr (ranging "from functional morphology down to biochemistry"; Mayr, 1982: 68). Falk (1988: 458-459), for instance, argued that species are to be conceptualized differently in evolutionary biology and in such research contexts as anatomy, physiology and behavioral biology:

> "(…) one has to distinguish between the contexts in which the term is used (…). In the context of the theory of evolution by natural selection a species is an individual (…). In other contexts species should be viewed as classes of objects that comprise natural kinds." (Falk, 1988: 455).

In a similar fashion, Kitcher (1984a; 1984b) agreed that the two fields distinguished by Mayr use different concepts and drew an even more radical consequence:

> "There are indeed two kinds of biological investigation that can be carried out relatively independently of one another, neither of which has priority over the other. These kinds of investigation demand different concepts of species. In fact (…) each main type of biological investigation subdivides further into inquiries that are best conducted by taking alternative views of the species category." (Kitcher, 1984a: 320).

According to Kitcher, at least nine different concepts should be distinguished, each appropriate to the research questions addressed in a particular subdomain of biological science. In Kitcher's view, however, these concepts constitute subconcepts of one overarching species concept (for discussion, see Section 3.3.2).

The above discussion showed that a distinction must be made between three epistemic roles that the term 'species' plays in contemporary biology: as denoting units of classification, units of generalization and units in evolutionary processes. These roles cannot be realized simultaneously, because in order to play tem all a concept must be able to meet incompatible demands. This agrees with the general observation made explicitly or implicitly by several authors (e.g., Kitcher, 1984a; 1984b; Endler, 1989; Williams, 1992; Kornet, 1993; Hull, 1987: 177-181; 1997; Shaw, 1998; Roselló-Mora, 2003, p. 324) that researchers impose particular demands on the concept of species that they use, depending on the research questions that are being addressed in a particular field of investigation, and that the demands posed in one context of investigation may well be incompatible to the demands posed in other contexts. Because of their incompatibility, in order to be able to play the three roles distinguished above the term 'species' needs to be interpreted as denoting multiple distinct scientific concepts, each finely tuned to the specific demands of the particular context(s) of biological research in which it features. In Section 3.2.2, I shall show that 'species' indeed denotes multiple distinct concepts and in Section 3.2.3 how the roles distinguished above map onto these concepts.

3.2.2. Ontologies of 'species'

A large number of definitions of the term 'species' have been advanced as (partial) solutions to the species problem and to accommodate the various roles of 'species' in biological investigation. An overview of the most important definitions available in the current literature has recently been provided by Mayden (1997; 1999); for a historical overview, see Lherminer & Solignac (2000). Contradicting De Queiroz' assertion quoted above, only under a minority of these definitions 'species' is understood as denoting a category of lineages or lineage segments. To give one obvious example, Mayr's widely endorsed *Biological Species Concept* conceptualizes species as populations rather than lineages (Mayr, 1942: 120).

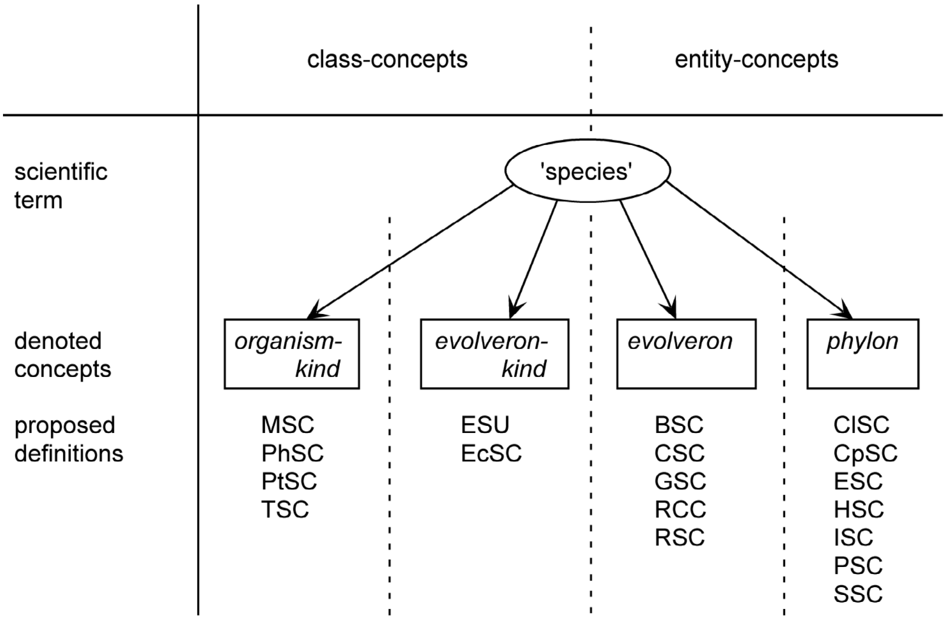

Figure 3.1: The term 'species' denotes four distinct scientific concepts. The most important definitions of 'species' are classified according to the concept to which they pertain. The following abbreviations are used: BSC = Biological Species Concept; ClSC = Cladistic Species Concept; CSC = Cohesion Species Concept; CpSC = Composite Species Concept; EcSC = Ecological Species Concept; ESC = Evolutionary Species Concept; ESU = Evolutionary Significant Unit; GSC = Genetic Species Concept; HSC = Hennigian Species Concept; ISC = Internodal Species Concept; MSC = Morphological Species Concept; PhSC = Phenetic Species Concept; PSC = Phylogenetic Species Concept; PtSc = Polythetic Species Concept; RCC = Reproductive Competition Concept; RSC = Recognition Species Concept; SSC = Successional Species Concept; TSC = Taxonomic Species Concept. For definitions and references to primary literature on these definitions, see Mayden (1997).

Then, what are the various ontologies that 'species' denotes? To provide an answer, I have considered the most widely endorsed and employed definitions of 'species' as listed by Mayden (1997; 1999). It was found that these definitions connect 'species' to four distinct ontologies, as drawn schematically in Figure 3.1. In two of the four meanings distinguished here, 'species' denotes a category of classes (in the same manner as 'element' denotes the category of classes contained in the Periodic System). In the other two meanings, 'species' denotes a category of spatiotemporally limited entities. Because of the fundamental differences between the ontologies involved, the four concepts associated with these ontologies cannot be understood as subconcepts of one all-encompassing species concept. That is, the fourfold distinction drawn here does not imply any form of species pluralism (for discussion of this issue, see Section 3.3.2). Consequently, new proper names have to be introduced to denote them. To emphasize the independence of the concepts, I use names that do not remind of 'species'[5]:

- *evolveron*: the term 'evolveron' denotes 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;[6]
- *phylon*: the term 'phylon' denotes 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*: the term 'organism-kind' denotes a category of classes of organisms; organism-kinds are classes of organisms that exhibit similar structural and/or behavioral properties;

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[5] Ereshefsky (1992; 1999) also suggested that the undifferentiated notion of species should lose its place in the conceptual framework of biological science in favor of a number of new notions. However, Ereshefsky's position stems from a wholly different analysis of the species problem. Whereas Ereshefsky holds that all concepts involved refer to a category of lineages (and thereby defends a form of species pluralism, as reflected in his use of the terms 'bio*species*', 'eco*species*' and 'phylo*species*'), in the view developed here there is no such ontological overlap between the four concepts at stake. (See Section 3.3.2.) Note also that the four terms introduced here at this stage are generic terms: for instance, various types of tree-segments have been proposed as candidates for being attributed species status and I do not now present an argument which of these is favored (i.e., which of these should be considered to constitute the category of phylons).

[6] However, not all populations are evolverons. Note that a system of populations is itself a population; cf. Dobzhansky's (1970: 357) remark that "Species are, (…) systems of populations (…). In short, a species is the most inclusive Mendelian population." See also the discussion by Mayr (1987). I use the term 'evolveron' in order to avoid the conceptual difficulties regarding the notion of population (a notion that is as historically burdened as the notion of species).

- *evolveron-kind*: the term 'evolveron-kind' denotes a category of classes of evolverons that occupy similar positions in evolutionary dynamics.

In the view presented here, the species problem is not a question of which of these four concepts should be taken as *the* species concept. As I show in the discussion below, all four concepts occupy a place in the conceptual framework of biological science.

It should be emphasized that I do not advocate the view that all four concepts *should* be incorporated in the conceptual framework of biological science. Rather, I present the diagnosis that at present they *are* in fact incorporated in this conceptual framework; whether their placement in the conceptual framework of biology will in the end prove legitimate, is a matter of whether the fields in which they are used will continue to find them useful.

(a) Two kinds of entities

The term 'species' is used in contemporary biology to denote two distinct kinds of spatiotemporally limited entities: dynamic entities (evolverons) and static entities (phylons).

The pioneers of the Modern Synthesis emphasized the dynamic meaning of 'species' (Dobzhansky, 1935; 1970: 357ff.; Mayr, 1942: 103; 1969: 26; 1982: 296). From the dynamic perspective that was developed in the Synthesis, species are entities that participate in evolutionary processes and interact as cohesive wholes with their environment and the other species therein, in the same manner as local populations do. That is, species understood this way are 'interactors' in the sense of Hull (1980), although Hull did not consider species to be interactors. (Williams, 1989, used 'evolvers' and counted species among the various sorts of evolvers.) Both Dobzhansky and Mayr were ambiguous on whether species should be understood primarily as populations (i.e., systems of interconnected organisms) or as systems of interconnected populations which in turn are composed of organisms, but they clearly saw species as entities that consist of organisms that live at a particular location and time. Under Mayr's *Biological Species Concept* species are explicitly conceptualized as systems of interconnected populations (Mayr, 1942: 120; 1969: 26; Dobzhansky, 1970: 23 & 357).

'Species' in the meaning of the evolveron concept plays an important role in several domains of present-day biological investigation, e.g., as denoting causal units in speciation studies and population biology (Williams, 1989; Shaw, 1998; Mayden, 1999: 105-106). Recently, Gould & Lloyd (1999) and Gould (2002: 597ff. & 704ff.) have also used 'species' as denoting evolverons in their discussions of a hierarchical theory of selection. Definitions of 'species' in the meaning of the evolveron concept include Mayr's (1942) *Biological Species Concept*, Templeton's *Cohesion Species Concept* and Paterson's *Recognition Species Concept* (for the latter two definitions, see Mayden 1997; 1999).

Researchers working in historical domains of biology commonly place emphasis on the static meaning of 'species'. Kluge (1990: 418), for example, argued that "(…) species are generally considered to be products of evolution (lineages), but not the units participating in processes." In this meaning 'species' denotes static segments of the tree of life, i.e., phylons, consisting of organisms that have lived in the past as well as organisms living in the present. (For other examples of this conceptualization of species, see Simpson, 1961: 152ff.; Hennig, 1966, Figure 6; Lidén & Oxelman, 1989; Ridley, 1989; De Queiroz, 1998: 60-61; 1999: 50-54). Phylons are objects of study in phylogeny reconstruction, where they feature as the building blocks of a historical pattern found in natural history. Attempts at defining the phylon concept include various extant *Phylogenetic Species Concepts*[7], as well as Hennig's (1966) definition, Kornet & McAllister's (1993) *Composite Species Concept*, Ridley's (1989) *Cladistic Species Concept* and Simpson's (1961) *Evolutionary Species Concept*.

The difference between evolverons and phylons can be illustrated by the distinction between 'species' as denoting synchronic entities and as denoting diachronic entities, that various authors have drawn parallel to the distinction between 'species' as denoting dynamic and static entities (see, for example, Salthe, 1985: 225-226; Endler, 1989: 627-628; Lee & Wolsan, 2002; Stamos, 2002; 2003: 67-74). According to these authors, two types of definitions of 'species' are available in the literature, that represent two perspectives on species: horizontal/synchronic definitions aim to identify species in a limited timeslice, while vertical/diachronic definitions aim to identify species as extending through evolutionary time.

While the above authors seem to understand the difference between horizontal/synchronic species and vertical/diachronic species as essentially a difference in perspective (Stamos, 2002: 176-178; 2003: 67, for example understands it as a difference in the temporal window that is taken), I believe that it is more than just a

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[7] Notwithstanding its name, the *Phylogenetic Species Concept* as advocated by Mishler & Theriot does not fall into this category of definitions, because it defines species as synchronic "monophyletic cross sections of a lineage" (Mishler & Theriot, 2000: 49). This definition can however be disregarded, since the concept of monophyly does not apply on the species level (as shown by Kornet & McAllister, 1993: 69-71).

difference in perspective: it is a difference in ontology. The synchronic-diachronic distinction maps onto the distinction between evolverons and phylons and is reflected in the composition of the two sorts of entities and the kinds of relations that exist between their parts. As synchronic entities, species are conceptualized as dynamic entities that take part in evolutionary processes, i.e., evolverons (see Salthe, 1985: 226; Endler, 1989: 627-628; Stamos, 2002: 176-177). They are systems of organisms, consist exclusively of synchronously existing organisms and derive their coherence from these organisms' abilities to interact, to influence each other's behavior, to determine the composition of later generations and to co-determine the behavior of the evolving entity. This conception of species is often implied in the view that species are individuals; as Holsinger (1984: 295) for example put it:

> "An individual (…) is an entity that, with respect to a particular process, behaves as a whole (…), i.e., with respect to the process being considered an individual is an entity that exists as a discrete unit, complete unto itself and coherent."

Species as diachronic entities, in contrast, are conceptualized as static segments of the tree-like pattern that represents the history of life on Earth, i.e., phylons (cf. Salthe, 1985: 225; Endler, 1989: 627-628; Stamos, 2002: 174-175; 2003: 67-68). They are the 'snail-trails' (Lee & Wolsan, 2002) or 'space-time worms' (Hull, 1997: 375; [1997] 2001: 207) left behind in history, extending over longer periods in time and consisting of organisms from both the past and the present. The parts of a diachronic entity are connected by historical relations that obtain between them: they are historical entities. Diachronic entities are not cohesive in the way synchronic entities are.[8] As an example, consider the prototypical biological entity: an organism. As a diachronic entity an organism includes all the cells from the past and the present that ever belonged to it; these cells belong to the diachronic entity because of ancestor-descendant relations between them. As a synchronic entity it includes only those cells, connected by metabolic interactions, that belong to it at one particular timeslice. Organisms as

[8] For recent discussions of cohesiveness as a requirement for individuality, see Ghiselin (1974: 538; 1997: 51-61) and Lee & Wolsan (2002: 653). Ereshefsky (1991) and Lee & Wolsan (2002: 656), among others, have pointed to the ontological difference between individuals and historical entities. Species individualism is discussed further in Section 3.3.1; see also Reydon (2003 – here the Appendix).

synchronic entities can take part as wholes in various kinds of processes (growth, metabolism, social interaction, etc.) in which their material composition co-determines how they behave: bodily composition at a particular time co-determines present and future energy requirements, for example. Organisms as diachronic entities do not take part as wholes in processes; after all, dead cells that are no longer part of an organism do not co-determine the behavior of the organism in the present.

Additionally, whereas evolverons as process entities continuously change their material composition as existing organisms die and new organisms are born into them, phylons as historical pattern entities have an unchanging material composition (once the pattern is finished, that is; phylons that incorporate organisms living and reproducing today constitute parts of history in the making).[9]

(b) Two kinds of classes

Next to the two kinds of entities discussed above, the term 'species' is also used to denote two kinds of classes: classes of organisms (i.e., organism-kinds) and classes of evolverons (i.e., evolveron-kinds). As discussed in Section 3.2.1, from the times of Aristotle to roughly the end of the 19th century the accepted ontology of species conceptualized species as essentialist natural kinds of organisms. Although with the Darwinian revolution the Aristotelian essentialist ontology of species was abandoned in the context of biological classification (Hull, 1965), the ontology of species as classes of organisms that share important properties continued to play its own role in particular contexts of biological investigation, such as Thompson's (1942) research program, the contemporary structuralist program (Goodwin, 1989; Webster & Goodwin, 1996; Goodwin, 1999) and the fields of microbiology (e.g., Roselló-Mora, 2003: 325), functional morphology and ecology (see, for instance, Kitcher, 1984a; 1984b; Hull, 1988: 213, note 2; Dupré,1993: 20; 2001; for a more radical view, see Ruse, 1998: 287). Definitions of the organism-kind concept that are still in use today include Sneath & Sokal's *Phenetic Species Concept* and Cronquist's *Morphological Species Concept* (for references, see Mayden, 1997; 1999).

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[9] In contrast to what is the case with organisms, as a historical pattern entity a phylon does not necessarily constitute the historical trace of precisely one evolveron. Because not all splitting events that occurred in the past in the tree of life can be recovered in the present (see Chapter 5, pp. 120-121), a given phylon will generally coincide with the historical traces of multiple evolverons that stand in ancestor-descendant relations to one another.

The ontology of species as classes of evolverons, evolveron-kinds, needs more discussion. 'Species' is used in various domains of biological investigation to denote groupings of independent evolutionary entities (i.e., evolverons that do not share a most recent common ancestor). In microbiology, for example, a widely used definition of species is "a group of strains (…), which have in common a set or pattern of correlating stable properties that separates the group from other groups of strains" (quoted in Rosselló-Mora & Amann, 2001: 52-53; but see Rosselló-Mora, 2003: 325, for a different viewpoint). This ontology of 'species' also features in the study of particular evolutionary processes, such as ecology-driven convergent and parallel evolution. Definitions of the evolveron-kind concept thus include for example Van Valen's *Ecological Species Concept* (see Mayden, 1997; 1999).[10]

A well-studied example in this latter context is the *Gasterosteus aculeatus* threespine stickleback complex. In a number of isolated Canadian lakes these sticklebacks occur in sympatric pairs of populations, one benthic and one limnetic population per lake, that are considered to have resulted from independent evolution in similar lake ecologies by way of deterministic and repeatable evolutionary processes (Schluter & McPhail, 1992; Schluter, 1998; Rundle *et al.*, 2000; Taylor & McPhail, 2000; Rundle & Schluter, 2004). The organisms from the benthic populations in different lakes exhibit a high degree of morphological and behavioral similarity; the same holds for the organisms from the limnetic populations in different lakes. Between

[10] An anonymous referee for the journal in which this chapter has been published commented that the interpretation of Van Valen's *Ecological Species Concept* as defining evolveron-kinds is questionable because according to this definition, species are lineages (i.e., phylons). While it is true that in Van Valen's definition "a species is a lineage (or closely related set of lineages)" (quoted in Mayden, 1999: 394), it is also the case that Van Valen explicitly holds that species are units that participate in evolutionary processes (1988: 49 & 57-60) and allows that one species may have more than one origin (1988: 57 & 63), counting units that occupy the same adaptive zone as members of the same species even if they do not share a most recent common ancestor. This suggests an ontology of evolveron-kinds (Van Valen introduced the ontological category of 'individualistic classes' as the ontology of species, but to me it is not clear how this ontology is to be understood). Because of Van Valen's emphasis on the occupancy of the same adaptive zone by separate evolving units, rather than on extent through time, I believe that Van Valen's definition should be read as defining evolveron-kinds (although the definition admittedly does also incorporate aspects of the phylon ontology).

benthics and limnetics clear morphological and behavioral differences exist. The benthic and limnetic populations that occur in sympatry within the same lake are reproductively isolated, but laboratory studies have shown hybridization between benthic and limnetic populations to be possible to a limited extent. Benthic-benthic and limnetic-limnetic interbreeding does not occur in nature because the populations are geographically separate, but laboratory studies have shown it to be fully possible.

In order to capture the phenomenon under study in this case, i.e., the deterministic (as emphasized by Taylor & McPhail, 2000) and repeated origin of independent instances of the same species under the same ecological circumstances and their stable persistence in sympatry with instances of closely related species, a conceptualization of 'species' as evolveron-kinds is required. As the following quotations show, two 'species' are recognized in this case, one encompassing the benthic populations from the different lakes and the other encompassing the limnetic populations:

> "Morphological and genetic evidence has been presented (…) to refute the possibility that the two sympatric forms merely represent a single-species polymorphism. The species have not been formally described, and we refer to them as 'benthic' and 'limnetic' on the basis of preferred foraging habitat (…). This is merely a convenience and is not meant to imply that the different populations of limnetics (or benthics) are monophyletic." (Schluter & McPhail, 1992: 87);

and:

> "(…) we have shown that reproductive isolation evolved in parallel under a common selective regime; this resulted in the repeated evolution of the "same" species in different lakes." (Rundle & Schluter, 2004: 209).

Here the conflict between the roles of 'species' in the contexts of classification and the study of evolutionary dynamics actually becomes visible (see Section 3.2.1). Whereas the study of repeatable evolutionary processes requires the recognition of two distinct classes of dynamic entities (evolverons), classification requires the recognition of uninterrupted segments of the tree of life. Genetic analysis has indicated that the various benthic populations do not share a common ancestor that is not shared also with the limnetic populations, and thus do not constitute the terminal points of a single uninterrupted tree-segment; the same holds with respect to the limnetic populations (Schluter, 1998: 120-121; Rundle *et al.*, 2000: 306; Rundle & Schluter, 2004: 200). For this reason, the researchers hesitate to formally attribute the status of species to "the classes 'limnetic' and 'benthic'" (Rundle & Schluter, 2004: 200-201; cf. Rundle *et al.*, 2000: 306), but use the term 'ecomorph' rather than 'species' to denote them and reserve the term 'species' for the units of classification. This practice is in accordance with the position defended here, that different terms should be used to denote distinct scientific concepts.

3.2.3. Mapping of roles on ontologies

As discussed in Section 3.2.1, the term 'species' performs three distinct epistemic roles in contemporary biology: that of evolutionary process units, of classificatory units in a general reference and retrieval system for biological science and of generalization-supporting units. Here I show how these roles are compatible with the four ontologies of 'species' distinguished above.

The role of evolutionary process unit presupposes an ontology of individuals that take part as wholes in natural processes. This role can thus be mapped directly onto the evolveron-ontology. The role of 'species' in the context of classification does not presuppose any particular ontology. It does however impose certain ontological requirements on the units that are used, such as stability through time and mutual exclusivity (Williams, 1992; Kornet, 1993). Whereas in the physical sciences the elements in the Periodic System (which possess a class-ontology) have been found to meet these requirements, in the biological sciences segments of the tree of life have been found suitable to function as the units of classification. Kornet *et al.* (1995; cf. Kornet, 1993), for instance, proved formally that the segments of the tree of life that Hennig identified as species meet the requirement of mutual exclusivity (although they do not meet other intuitions regarding species). Thus, the classificatory role of 'species' is to be attributed to the phylon concept.

The role of 'species' as denoting units of generalization presupposes a class-ontology, because spatiotemporally limited entities cannot serve as the foundations of universal scientific generalizations (cf. Hull, 1978: 353-355). Current accounts for this role divide into two types that pertain to different levels of organization. First, there are investigators who retain the traditional understanding of species as natural kinds of organisms, i.e., as groups of organisms that exhibit the same structural and behavioral properties because of a shared intrinsic nature. In this role, which lies at the basis of for instance the structuralist research program (Goodwin, 1989; Webster & Goodwin, 1996; Goodwin, 1999), scientific generalizations over species of organisms are supported by shared intrinsic properties: "(…) the notion that species taxa are historical individuals (…) must be extended to some concept of organisms as entities with necessary natures which define their intrinsic properties, allowing the construction of a rational taxonomy of biological forms as well as a historical genealogy." (Goodwin, 1999: 398 – note that Goodwin presupposes that a single concept is able to function in both the contexts of classification and generalization). Accounts like this pertain to the organismal level of organization and map the role of units of generalization onto the organism-kind concept. Second, it has recently been attempted to ground the role of species as generalization-supporting groups of organisms in external evolutionary factors rather than the intrinsic nature of organisms (an important example is Boyd, 1999). Accounts like this consider the evolutionary properties of groups of organisms, rather than of individual organisms, and thus pertain to the organizational level of clusters of organisms. (For instance, according to Boyd, 1999: 165-167, species are to be conceptualized as natural kinds with populations as their members). I shall extensively address the issue of species as units of generalization elsewhere (Chapter 5).

3.3. Two cases of conceptual conflation

In the previous section, I argued for the thesis that the term 'species' denotes multiple distinct scientific concepts by way of an epistemological and ontological analysis of the term. In this section, this claim will be strengthened by considering two examples from recent thought on the species problem: species individualism and species pluralism. My aim is to illustrate how these positions both stem from and propagate a mistaken understanding of the species problem, and to show that these two positions consequently cannot be maintained.

3.3.1. Species are not always individuals

Species individualism – the position that 'species' always denotes a category of concrete entities with organisms as their parts rather than abstract classes having organisms as their members – is commonly perceived as a decisive step toward the final resolution of the species problem (the *loci classici* are Ghiselin, 1966; 1974 and Hull, 1976; 1978). Species individualism is however a problematic position. For one, as an ontological solution to the problem species individualism is insufficiently articulated. Whereas for instance some authors combine species individualism with an ontology of species as evolverons, others combine species individualism with a conceptualization of species as the basic segments of the tree of life (phylons).[11]

A more important problem, as is argued below, is that species individualism has its roots in the widely held assumption that only one single scientific concept is at stake in the species problem. This is problematic, because acceptance of this assumption causes participants in the discussion to focus on the role of the term 'species' in the context of the dominant theory in contemporary biology, thereby ignoring the roles of 'species' in other (possibly less prominent) contexts of biological work.

That the abovementioned assumption underlies species individualism can be seen from the way in which the classic arguments in support of species individualism are construed. As exemplified by Hull's (1976: 175) formulation of the issue – "But what are species *really*: classes or individuals?" – in these arguments the question is essentially understood as the search for the one true nature of species (cf. a remark by Dupré, 1993: 51, to this extent). This problem is subsequently construed as a simple dichotomy: either species are to be attributed individual-status, or species should be attributed class-status. By focusing on the role of the notion of species in evolutionary theory, against the background consideration that the theory of evolution constitutes the core of present-day biology (see Ghiselin, 1974; Hull, 1978; 1988: 213ff.; Dupré, 1993: 20; Webster & Goodwin, 1996: 31ff.), the dichotomy is then resolved. From the viewpoint of evolutionary theory, so the argument goes, 'species' denotes the products of evolution, or the things that take part in evolutionary processes, or both (the classic arguments differ in the details). As such, species cannot be conceptualized as classes or sets of organisms, since classes and sets as abstract objects can neither be the products of real natural processes nor participate in them. And if species cannot be classes or sets, then following the above dichotomy they must be individuals. Hull's claim in one of the classic papers on the topic is, correspondingly, that "(…) evolutionary theory requires a (…) shift in the ontological status of species as units of evolution. Instead of being classes, they are individuals." (1976: 175).

[11] Interestingly, Ghiselin and Hull take conflicting views on the ontology of species: Ghiselin (1974: 537-538; 1997: 13-16) seems to conceptualize species as dynamic entities, whereas Hull (1978; 1980; 1988: 215; 1999: 42-43; [1997] 2001: 206-207) conceptualizes species as static entities (more precisely, lineages).

Neither the construal of the species problem as an 'either-classes-or-individuals' dichotomy nor the argumentation for species individualism from the explicit perspective of evolutionary theory do justice to the diverse nature of biological science: biology consists of various contexts of investigation in which various research programs are at work, all of which use the term 'species' for various purposes but not all of which necessarily work from an evolutionary perspective (see also Reydon, 2003 – here the Appendix).[12] Well-known examples are those research programs that search for general principles underlying organismal form, such as the structuralist program mentioned earlier, and domains of biological investigation that study organisms as functional systems, such as functional morphology and ecology (see Dupré, 1993: 42-43; 2001: 218). And although present-day systematic biology does aim to ground biological classification in evolutionary history, it is not by necessity that systematic biology works from an evolutionary perspective. Although, as Dobzhansky (1973) famously argued, no account of biological phenomena is complete without an account of the evolutionary history and the evolutionary processes involved, this does not mean that all of biological science must necessarily take an evolutionary perspective on all the phenomena under study: parts of the account may be obtained without taking an evolutionary perspective.[13] Correspondingly, of the three roles of the term 'species' distinguished in Section 3.2.1, only the role of 'species' as denoting evolutionary process entities explicitly presupposes an ontology of species as individuals that feature in accounts of the evolution of life on Earth.

Both the construal of the species problem as a straightforward 'either-classes-or-individuals' dichotomy and the argument from evolutionary theory implicitly

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[12] The question whether evolverons and phylons can both be counted as belonging to the same ontological category, the category of individuals, continues to be a topic of some debate. According to for instance Ereshefsky (1991) and Lee & Wolsan (2002: 656) a third category (the category of historical entities) is needed to account for the difference between the two sorts of entities (while Ereshefsky holds that species fall in the category of historical entities, Lee & Wolsan place them in the category of individuals). Similarly, Mayr (1987) has argued that the issue cannot be seen as a simple individuals-or-classes dichotomy. According to Mayr, species cannot be conceptualized as either individuals of classes but belong to the category of populations.

[13] A similar point is implied in Mayr's (1961) classic assertion that biology is concerned with both proximate (mechanistic) and ultimate (evolutionary) explanations of the phenomena under study.

presuppose that 'species' denotes one single scientific concept. That this approach to the problem does not do justice to the actual situation in biological science indicates that the presupposition on which it is based is not well taken.

3.3.2. Homonymy, not pluralism

In recent decades pluralism has become a major trend in dealing with the species problem. Several authors have suggested pluralist approaches to the problem, which however differ considerably both in content and with respect to the argumentation presented in support. A clear understanding of what species pluralism encompasses and how it is different from species monism is still lacking. Hull recently characterized the situation thus:

> "One problem unfortunately characteristic of such contrasts as monism versus pluralism is that the apparent differences between them tend to disappear under analysis. Numerous senses of monism blend imperceptibly into just as many senses of pluralism. (…) A clear contrast exists between more simplistic notions of monism and pluralism, but no one seems to hold any of these simplistic alternatives. When pushed, most authors retreat to some platitudinous middle ground." (Hull, 1999: 24; cf. 1997: 358).

Mishler & Brandon (1987: 403), for example, qualified their position as being "pluralistic only during the transition as a prevailing monistic concept is broken up" into "a greater number of explanatory concepts, each quite monistic within its proper domain". In a similar fashion, Ereshefsky (1992: 688) remarked that: "Some may view eliminative pluralism as just a complicated form of monism. If that is the case, then the arguments (…) have been successful." I believe that species pluralism constitutes more of an obstacle than a helpful tool in the resolution of the species problem, not only because it is unclear what exactly is meant by the various versions of species pluralism that have been advanced in the literature, but more importantly because – as I shall argue – species pluralism stems from an inherently wrong approach to the species problem.

Two types of pluralism can be distinguished, which I here call *definitional pluralism* and *conceptual pluralism* (for this distinction see also Mishler & Brandon, 1987: 402ff; Williams, 1992: 319). Both presuppose the existence of a single overarching concept of species in biology.

Species pluralism as definitional pluralism holds that for different groups of organisms different natural processes are responsible for the origin and maintenance of species and that consequently the attribution of organisms to species should rest on different grounds in different domains of biodiversity. Whereas some species of organisms are for instance kept together by way of assortative mating, others derive their coherence from, say, postzygotic isolation. In order to reflect this natural state of affairs, from the perspective of definitional pluralism it is necessary to employ different definitions of 'species' – which itself is understood to denote a single concept – when studying different sections of biodiversity. However, for each group of organisms there is a single best partition into species, applicable in all contexts of scientific investigation: "(…) a single, optimal general-purpose classification exists for each particular situation, but (…) the criteria applied in each situation may well be different" (Mishler & Brandon, 1987: 403; see also Mishler & Donoghue, 1982: 500-501). Definitional species pluralism is pluralistic with respect to the definitions associated with the concept of species but monistic with respect to the concept itself.

Definitional pluralism however fails to address the nucleus of the species problem: what lies at the heart of the problem is not just that *different* organisms cluster by means of different mechanisms into different kinds of units called 'species', but that there are different ways for attributing *the same* organisms to so-called 'species' that play different roles in different contexts of biological investigation (cf. Section 3.2.1). While there still remains some discussion whether or not different species definitions generally yield the same groupings of organisms (for instance Ghiselin, 1997: 130 *versus* Ruse, 1998: 288), there is ample empirical evidence that they often do not. Recent empirical examples of how different species definitions yield different groupings of organisms are given by Gleason *et al.* (1998) and Agapow *et al.* (2004); other examples include the various well-known instances of sibling species and polytypic species (Mayr, 1942; 1982: 281-282 & 298ff.).

Species pluralism as conceptual pluralism acknowledges that the same organisms can be grouped into so-called 'species' in multiple ways. It rejects the assumption that all biologically interesting questions regarding a given group of organisms can be addressed by using a single concept of species. The positions advocated by Kitcher (1984a; 1984b) and Ereshefsky are forms of conceptual pluralism:

> "The forces of evolution produce at least three basal lineages (…) that *cross classify* the organic world. (…) Each of these lineages is equally important in the evolution of life on this planet. (…) Consequently, the tree of life on

> this planet is segmented into *a plurality of incompatible but equally legitimate taxonomies*." (Ereshefsky, 1992: 679, emphasis added; cf. Ereshefsky, 1991: 100; 1998: 106; 1999).

According to Ereshefsky, the study of the different evolutionary forces that shape the tree of life requires different, incompatible but equally legitimate partitions of the tree of life, thus entailing the use of multiple distinct concepts, one for each partition (Ereshefsky, 1992: 676-677; 1999: 292-294). Ereshefsky's version of species pluralism as conceptual pluralism thus understands the term 'species' as the placeholder for multiple distinct scientific concepts that have, however, one thing in common: in the end they all are *species* concepts in that they share the same ontology (i.e., the phylon ontology) and occupy similar positions in biological theory (i.e., as units of classification). Kitcher's version of pluralism rests primarily on overlap in the roles – rather than in the ontology – of the different concepts in biological theory as representing the various "biologically interesting relations" that can exist between organisms (Kitcher, 1984a: 309). (Note, however, that Kitcher's rejection of species individualism and his assertion that "the relation between organism and species can be construed as the familiar relation of set-membership" (1984a: 309) rather than the part-whole relation, do suggest that Kitcher's pluralism also presupposes some ontological overlap between the concepts at stake.)

What in my view is wrong with conceptual species pluralism is precisely what makes it an instance of pluralism. Species pluralism (in both its guises) 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 all in some respect are of the same kind.) Ereshefsky, for instance, (incorrectly) interprets the diverse sorts of species concepts advocated in the literature as all assuming that species are lineages and asserts that "(…) this assumption is essential for any post-Darwinian definition of the species category." (1992: 674). And Mishler and co-workers argue for a form of definitional pluralism from the implicit presupposition that species concepts should identify taxa in the context of phylogenetic theory (Mishler & Donoghue, 1982: 494 & 501; Mishler & Brandon, 1987: 405 & 412; Mishler & Theriot, 2000: 44 & 54).

The problem with the presuppositions like the above, underlying species pluralism, is threefold. First, advocates of species pluralism do not provide any foundation for adopting presuppositions like the above. Second, adopting such a presupposition may easily (and usually does) result in a biased view of the nature of 'species'. This bias is perhaps most clearly exemplified by Ereshefsky's (1992: 688) statement that "By allowing nonhistorical species concepts, Kitcher's pluralism falls outside the domain of evolutionary biology and should be rejected." Based on the implicit presupposition that all species are ultimately the same sort of units (in this case: phylogenetic tree-segments), Ereshefsky thus *a priori* denies a place in the conceptual framework of biology to any concept under which species status is attributed to units other than segments of the tree of life. In a similar spirit, Sober objected against Kitcher's recognition of non-historical species concepts next to historical concepts:

> "The danger is that we are apt to take seriously a possible interpretation of the species concept that no longer plays a role in evolutionary theorizing. (…). It isn't that this interpretation is a priori incapable of theoretical development. It's just that is currently constitutes a mere hope and lacks any serious degree of theoretical articulation" (1984: 334).

Sober thus a priori excludes non-historical concepts from the domain of concepts that could legitimately be attributed species status.

Third, and most importantly, such presuppositions are in conflict with the actual situation in biology, as the findings of Section 3.2 show. For pluralism based on functional (epistemic) overlap to be correct, the four concepts at stake should perform similar functions in biological theory and explanation: they should all refer either to classificatory units, or to process entities, or to units of generalization. As discussed in Section 3.2.1, this is not the case and the four concepts perform very dissimilar functions. And as I have argued in Section 3.2.2, there is also insufficient ontological overlap between the four concepts to consider them as subconcepts of one overarching species concept. The understanding of the species problem as a case of pluralism, thus, is insufficiently founded, entails a biased perspective on the species problem and is not adequate to the actual state of affairs in biological science.[14]

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[14] In this context, it is important to note that the issue of functional and ontological overlap is not a matter of the material extension of the various concepts: even if in a particular case an evolveron and an organism-kind would consist of exactly the same organisms, the two still are fundamentally different sorts of clusters that feature in different contexts of biological theory and explanation.

Because of the lack of epistemic or ontological similarity between the four concepts at stake in the species problem, I believe that the species problem is better understood as a case of homonymy rather than pluralism. To see the difference, the formal distinction between pluralism and homonymy is important: while pluralism presupposes some similarity between the concepts or definitions at stake, in cases of homonymy this similarity is wholly absent and the term is understood as denoting multiple independent concepts. It is this presupposition – and the a priori judgment that comes with it – that distinguishes species pluralism from the position taken in the present chapter, which should not be mistaken for yet another form of species pluralism.

The difference is crucial for a clear perspective on the species problem, for 'pluralism' refers to a philosophical position that can be adopted and defended, whereas 'homonymy' refers to the diagnosis of an existing situation that needs to be remedied. Correspondingly, pluralism and homonymy have very different implications for how we should approach the species question and call for different lines of action. On the adoption of species pluralism the concept of species (and the category to which it refers) is retained as part of the conceptual framework of biological science and the main issue to be addressed is to provide an account how its different subconcepts are connected. In contrast, the diagnosis of homonymy calls for abandoning the concept and the category to which it refers altogether and to insert a number of new concepts and categories into biology's conceptual framework. The main challenge then is to establish the various meanings in which the term 'species' in fact is used and subsequently to assess the various concepts involved for their scientific value and material reference. By adopting an a priori perspective on the ontological nature of species, species pluralists are bound to ignore some of the various meanings that 'species' actually possesses.

A comparison of Ereshefsky's version of pluralism with the position defended here shows how the implications of the two positions differ. At first sight, Ereshefsky's (1998; 1999; cf. note 5) suggestion to replace the undifferentiated notion of species by a number of new notions (biospecies, ecospecies, phylospecies) could be understood as a call to abandon the concept of species and to replace it by a number of other concepts in biology's conceptual framework. However, Ereshefsky's suggestion amounts to abandoning the *term* 'species' but not the concept and the category of units that used to be attached to the term. Notwithstanding Ereshefsky's (1998: 113; 1999: 290-295) assertion that "(…) there is no unified ontological category called 'species'", from the perspective of his version of species pluralism the species category in fact is not wholly disunified either (as it is from the perspective defended in this chapter). After all, on Ereshefsky's account the units called 'species' are ultimately of the same sort: all are basic lineages that have come into being as a consequence of different forces of evolution and all function in the same manner in the study of these different forces. Hence, it is indeed the case that *if* conceptual species pluralism is correct, it is indistinguishable from monism, since all concepts associated with the species category can be understood as special instances of one underlying concept (such as the *General Lineage Concept* suggested by De Queiroz, 1998; 1999). In this sense, meaningful talk of 'species' and the species category remains possible under Eresfefsky's pluralism. By introducing a number of new notions to take the place of the old notion of species, Ereshefsky refined the old notion but did not abolish it.

In sum, species pluralism constitutes an approach to the species problem that is not well founded, entails a biased perspective on the nature of species and does not accord with the actual state of affairs in biology.

3.4. Concluding remarks

None of the approaches to the species problem proposed in the literature have so far been able to put the problem to rest once and for all. An alternative approach is thus called for. The preceding discussion of species individualism and species pluralism served to show that these two widely followed ways of approaching the species problem rest on a mistaken understanding of the nature of the species question as involving just one scientific concept. Taking this perspective obstructs the resolution of the problem, since it tends to disregard both the variety of incompatible roles played by the term 'species' in biological science and the variety of ontologies involved in fulfilling these epistemic roles. If nothing else, the troubles with species individualism and species pluralism indicate that 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.

My central claim in this chapter was twofold: (1) contrary to what has been suggested, the present-day species problem in philosophy of biology is far from being resolved and (2) this situation is primarily due to the homonymic nature of the term 'species'. The explication given here of the four ontologies denoted by the term 'species' merely constitutes the first step in resolving the species problem. A full resolution of the species problem requires a thorough epistemological and ontological analysis of the positions in the conceptual framework of biological science occupied by the concepts distinguished here. Although regarding the phylon concept this work has already been done (see Kornet, 1993; Kornet & McAllister, 1993), regarding the other three concepts distinguished above much work still is left to be done.

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