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"The species problem has to do with biology, but it is fundamentally a philosophical problem (…) [W]e often fail to solve our problems because we cannot even identify them. Under such circumstances, conceptual investigations do more than just help. They are the only way out."

Michael T. Ghiselin (1974). A radical solution to the species problem.
Systematic Zoology 23: 536-544 (pp. 541 & 543).

"Professor Van Iersel las de eerste versie van mijn proefschrift en had daar 134 opmerkingen bij. Vele middagen discussieerde ik met hem over die, elk voor zich, zeer zinnige opmerkingen. Daarna verwerkte ik ze en leverde de, naar ik hoopte, sterk verbeterde tweede versie in van mijn proefschrift. Hij las die en had daar 204 opmerkingen bij. Het zijn er zeventig meer dan bij de eerste versie, dacht ik hoogst verbaasd. (…) [I]k verwerkte ze en leverde de derde versie van mijn proefschrift in. Hij had 254 opmerkingen. Wel verdraaid, dacht ik, het worden er steeds meer."

Maarten 't Hart (1984): *Het Roer Kan Nog Zesmaal Om*,
Amsterdam: De Arbeiderspers, pp. 69-70.

Contents

1 General introduction

1.1. The species problem

Charles Darwin concluded the *Origin of Species* on an optimistic note:

> "When the views entertained in this volume on the origin of species (…) are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history. Systematists (…) will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. (…) The endless disputes whether or not some fifty species of British brambles are true species will cease." (Darwin, 1859: 484).

In the time that has passed since the publication of the *Origin of Species*, Darwin's optimism has however proved unjustified: Darwinian evolution has become generally accepted, but the disputes in biological science regarding the correct partitioning of organismal diversity into species continue as before.

That these disputes have not subsided, is primarily due to a persistent lack of clarity regarding one of the central terms in biological science: 'species'. Notwithstanding the large amount of work that has been done in attempts to clarify the nature of those things or classes that biologists call 'species', as well as the criteria by means of which species can be delimited in nature and organisms can be allocated to species, the lack of clarity still persists. What has come to be known as 'the species problem' essentially consists of two distinct, but intricately interwoven, issues, one ontological and the other epistemological. In the present dissertation, emphasis lies first on the ontological side of the species problem, before turning to epistemological issues.

For a variety of reasons it is important to address the species problem in the context of the present state of affairs in biological science. One reason pertains to the foundations of biological science. Without a clear perspective on what the term 'species' refers to, how and in how many ways the units called 'species' function in biological research and how these units can be delimited in practice, biological science itself is lacking an essential part of its foundations. Contributing to resolve the conceptual side of the species problem is one of the principal tasks of investigators in the foundations of biological science.

Another fundamental reason pertains to the advancement of philosophy of science. Philosophy of biology, as I perceive it, stands with one leg in biological science and with the other leg in general philosophy of science, in that the issues that are addressed in the field of philosophy of biology have direct consequences for both these

fields of investigation. This is also the case with respect to the species problem. Issues from general philosophy of science, such as the nature of scientific explanation and of scientific kinds, epistemological and ontological issues regarding natural kinds, the nature of individuality and the question what sorts of things there are in the world, all can be tackled using the species problem as a case study, entailing new insights into these issues (as the following chapters show).

The work on the species problem presented here is also relevant for the current biodiversity crisis. Faced with the rapid extinction of biodiversity on Earth, much effort is put into evaluating how diverse life on Earth actually is, how rapidly extinction actually proceeds and how extinctions can be countered. Usually, these efforts hinge on a notion of species: biodiversity is measured in terms of the number of species and species are understood as the units that become extinct and are worthy of conservation. A better understanding of the nature of 'species' directly affects our assessment of the state of biodiversity on Earth and thus can direct human actions in relation to the biodiversity crisis.

The present dissertation aims to contribute to resolving the species problem in its contemporary form by addressing two aspects of the problem. First, the nature of the species problem is examined and it is shown that the species problem is deeper than is commonly thought: when considering the ontological reference of the term 'species', it is found that multiple independent scientific concepts – rather than one single concept – are at stake. Second, one of the epistemic roles of 'species' in biological science is elaborated in detail: the role of 'species' as referring to units of generalization, that is, as denoting kinds of organisms over which explanatory and predictive generalizations hold. The following section gives an outline of the steps taken in addressing these issues.

1.2. Outline and summary of the present dissertation

In ***Chapter 2***, a first exploration of the nature of the species problem is undertaken. The species problem has attracted the interest of biologists and philosophers from times well before Darwin's lifetime up to the present day. By now, the volume of literature that has been published on the issue has grown to immense proportions. Then, one may legitimately wonder, why has the problem not been solved long ago? Why is it that every year still new papers and books (including the present dissertation) that address this issue see the light?

Several authors who have considered the species problem have suggested various reasons for the persistence of the problem. Some have argued that the resolution of the problem has been hampered by an undue emphasis on the philosophical aspects of the matter and that the best approach to take is to gather more empirical data regarding the organismal world. Others have countered that deeper philosophical analysis, rather than more empirical investigation, is the adequate approach. In contrast to these suggestions, I take the view that neither the empirical aspects of the species problem nor the philosophical issues that it encompasses constitute the principal reason for the problem's persistence. Rather, they are the symptoms of what I believe is the underlying reason why the species problem has to the present day resisted a resolution: the failure to recognize that the term 'species' does not refer to one single scientific concept, but has during the development of biological science become a placeholder for a number of *independent* concepts. In sum: in present-day biology, 'species' is a homonymic term.

While in Chapter 2 this perspective on the species problem is only suggested and is compared to the suggestion that was recently advanced in the literature, that 'species' is a family resemblance concept (in that all actually existing species resemble each other in various ways, while there is no property common to them all), in ***Chapter 3*** it is argued and elaborated in detail. In this chapter, an epistemological and an ontological analysis of the term 'species' are conducted.

When considering the epistemic roles in which the term 'species' features in contemporary biological science, three distinct roles are identified: species function as units of taxonomic classification (i.e., units in the general reference system that biologists use to order the specimens they study), units of generalization (i.e., kinds of organisms over which explanatory and predictive scientific generalizations can be made) and units of evolution (i.e., the entities that participate in evolutionary processes and undergo evolutionary change). Contrary to what is widely (usually implicitly) assumed, there is no a priori reason why these three roles should all be performed by a single scientific concept. In fact, as is argued in this chapter, the requirements that these roles impose on the concept that is to play them are not always compatible, implying that more than one concept is needed to play these roles.

The examination of the ontology of the term 'species' that is conducted in Chapter 3 reveals that as it is used in present-day biology this term indeed denotes multiple distinct concepts. During the development of biological science, 'species' has come to denote four distinct sorts of referents: cohesive systems of synchronously living organisms that participate as wholes in evolutionary processes; segments of the phylogenetic tree of life that consist of both past and present organisms that are

connected by means of ancestor-descendant relations; classes of evolutionary units (that is, classes that have systems of synchronous organisms as their members); and classes of organisms that share particular structural or behavioral properties. These four sorts of referents are ontologically very different, implying that they cannot be subsumed under a single scientific concept and that four distinct concepts are at stake in the species problem. In short, 'species' as currently used is a homonymic term that functions as the placeholder for four independent scientific concepts, each referring to a particular ontological category.

It should be emphasized that I do not propose that all four concepts *should* be incorporated in the conceptual framework of biological science. Rather, I present the diagnosis that the four concepts identified in Chapter 3 *are* in fact incorporated in the present-day conceptual framework of biology. Whether their placement in this conceptual framework will in the end prove necessary is an empirical matter, rather than an issue to be addressed by conceptual analysis.

After having established this state of affairs, its consequences are drawn for two ideas that determine much of contemporary thought on the species question: species individualism and species pluralism (also in Chapter 3). It is shown that both these positions rest on the (usually implicit) assumption that the term 'species' stands for one single scientific concept (be it in the case of pluralism an overarching concept that can be refined into a number of distinct but interconnected subconcepts). As such, neither species individualism nor species pluralism match the actual state of affairs in biological science, in which 'species' is used to denote four independent concepts. My conclusion is therefore that the adoption of species individualism and/or species pluralism stands in the way, rather than helps, when addressing the species problem.

Species individualism in particular is widely adopted by both biologists and philosophers of biology. It is again addressed in the ***Appendix***, where I show that a recently published defense of species individualism fails on several counts.

The last two chapters of this dissertation focus on one of the three roles of species identified in Chapter 3: the role of species as units of generalization. In ***Chapter 4***, which contains the spin-off for general philosophy of science of the work presented in this dissertation, the nature of scientific generalizations and kinds is considered. On the traditional view in philosophy of science, scientific explanation and prediction essentially consist in the making of well-founded generalizations. Observed similarities in the properties of different entities, for instance, are explained by identifying these entities as belonging to the same natural kind and thereby subsuming them under a generalization of the type 'All (or most) entities of kind *K* exhibit property *p*.' In a

similar fashion, unobserved properties of present and future entities of a particular kind are predicted by means of a generalization stating that if a particular entity would be a member of kind *K*, it would (with a high probability) exhibit a particular property or set of properties. In this chapter, it is shown that two sorts of generalizations are required to explain and predict the similarities that organisms exhibit in their structural and behavioral properties.

It is widely assumed that all of scientific explanation and prediction takes place in terms of universal laws of nature. In contrast, the considerations in Chapter 4 show that two fundamentally different sorts of generalizations play a role in scientific explanation and prediction: law-generalizations and kind-generalizations. Law-generalizations pertain to changes in states of affairs and do not directly invoke scientific kinds; kind-generalizations pertain to the properties that material entities exhibit and hold over the members of kinds of entities.

An examination of kind-generalizations shows that two sorts of scientific kinds exist, over which explanatory and predictive generalizations hold that rest on different types of underlying factors: spatiotemporally unlimited causal kinds, over which generalizations hold that rest on causal mechanisms to which their member entities are subject, and spatiotemporally limited historical kinds, over which generalizations hold that rest on the shared history of their member entities. The nature of the factors that underlie generalizations over the members of causal kinds is such that these generalizations may be exceptionless, but may also exhibit exceptions. Similarly, the nature of the factors that underlie generalizations over the members of historical kinds is such that historical generalizations may exhibit exceptions, but may also be exceptionless.

From these findings it follows that the common use of the criterion of universality to evaluate the scientific validity of all proposed explanations and to assess the scientific status of scientific disciplines, is incorrect. Whereas the criterion of universality is appropriate for explanations in terms of law-generalizations, it is misplaced for explanations in terms of kind-generalizations. Explanations and predictions of similarities in the properties of material entities rest on kind-generalizations that should not be assessed in terms of universality. This means that the widespread view that valid scientific explanations and predictions can only rest on exceptionless, spatiotemporally unlimited generalizations, is incorrect.

A consequence is that the scientific status of biology should be seen in a novel perspective. Generally, biology is contrasted with the physical sciences with respect to explanatory and predictive content. Whereas the physical sciences deal in universal

generalizations (that is, laws of nature) that serve as the basis of valid scientific explanations and predictions, so the argument goes, the generalizations of biology are non-universal and therefore cannot by themselves support scientific explanations and predictions. Biology, it is then concluded, cannot produce explanations of its own but uses explanations and predictions that rest on the laws of the physical sciences. This argumentation is now found wanting: biology does possess explanatory and predictive generalizations of its own, which however should not be assessed in terms of universality (as is the case with all kind-generalizations).

Chapter 4 constitutes a forerunner of ***Chapter 5***, in which the role of species as units of generalization in biological science is considered. Paul Griffiths and Ruth Millikan have recently argued that species, on the adoption of the ontology of species as segments of the phylogenetic tree of life, can and should be conceptualized as scientific kinds over which explanatory and predictive generalizations hold. Contrary to Griffiths' suggestion, I argue that the ontology of species as phylogenetic tree-segments intrinsically conflicts with any possible conceptualization of species as natural kinds (which, from the perspective taken in the present dissertation, are contained in the category of causal kinds). Furthermore, in this chapter it is found that not all sorts of species-level tree-segments can be conceptualized as historical kinds of organisms. This is possible only under one particular definition of species as segments of the tree of life, i.e., the *Composite Species Concept*.

1.3. Concluding remark

The chapters in the present dissertation have been written in different stages of investigation. As a consequence, they reflect changes that my understanding of the present-day species question has undergone. One example is the following. While in Chapter 3 I assume that the role of species as units of generalization presupposes that species possess a class ontology, in Chapter 5 I show that this role of species is well compatible with an ontology of species as spatiotemporally limited historical entities: under the *Composite Species Concept*, phylogenetic tree-segments can be conceptualized as historical kinds – that is, units of historical generalization. This finding, in turn, entails another result that is unforeseen in Chapter 3. In that chapter, it is argued that more than one concept is needed to perform the three epistemic roles of 'species'. The *Composite Species Concept* was initially devised to provide a definition of species as units of classification but as it now turns out, the *Composite Species Concept* defines

entities that can simultaneously perform two of the epistemic roles of 'species' in contemporary biology: that of units of historical generalization and of units of classification.

Reference

Darwin, C. R. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.

2 A first exploration: Why does the species problem still persist?

Abstract

Despite many years of discussion, the species problem has still not been adequately resolved. In this chapter, the question is addressed why it is the case that the species problem has come to persist to the present day. Two recently suggested answers to this question are discussed that place the blame on the species problem's empirical aspects or on its philosophical aspects. In contrast, I argue that neither of these two faces of the species problem constitutes the principal cause of the species problem's persistence. Rather, they are merely symptoms of the real cause: the species problem has not yet gone away because of a failure to recognize that not one but a number of distinct concepts are at the heart of the problem. To illustrate this point, a recently proposed solution to the problem is examined: the suggestion to understand the concept of species as a family resemblance concept.

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2.1. Introduction

Almost half a century ago, in his preface to a special symposium volume on the species problem, the biologist Ernst Mayr summarized the situation with respect to the issue thus:

> "Few biological problems have remained as constantly challenging through the past two centuries as the species problem. Time after time attempts were made to (…) declare the species problem solved either by asserting dogmatically that species did not exist or by defining, equally dogmatically, the precise characteristics of species. Alas, these pseudosolutions were obviously unsatisfactory." (Mayr, 1957: iii).

Unfortunately, Mayr's words still apply today; several dozens of competing definitions of the notion of species are readily available in the literature (for a sample, see Mayden, 1997), but no solution has yet been found that can put the species problem to rest once and for all.

Since the species problem has certainly not suffered from a lack of attention, one may wonder why it is that the problem still continues to persist and whether a definitive solution is at all possible. By way of background to the work presented in the following chapters, here I address this question by considering two issues. The first (Section 2.2) pertains to the nature of the species problem. In recent discussions of this topic (e.g., Hey, 2001a; 2001b; Pigliucci, 2003), the problem's empirical side and, alternatively, its philosophical aspects have been advanced as the primary factors responsible for the problem's persistence. In contrast, I suggest that the empirical and philosophical issues that arise in the context of the species problem are, in most cases, merely the symptoms of the real reason why the species problem continues to resist a definitive solution. This underlying reason is the failure to recognize that the problem is not one regarding a single scientific concept, the concept of species, but rather one that involves a number of distinct scientific concepts, conflated under the same name. In other words, 'species' is a homonymic term. I extensively discuss this position (which has been implicitly pointed out earlier by Kornet, 1993) in Chapter 3 (Reydon, 2005) and I shall outline it only briefly here. The second issue considered here (Sections 2.3 & 2.4), as an illustration of the above point, is the recent proposal that the species problem can be resolved by understanding the notion of species as a family resemblance concept.

I argue that because of the failure to distinguish between the different meanings of 'species', this proposal cannot yield a final solution to the problem.

2.2. Why is the species problem still here and whose problem is it anyway?

Recently, it has been questioned why the species problem continues to persist, rather than having been resolved already decades ago. Hey (2001a; 2001b), for example, suggested that a wrong approach to the species problem had been taken all along: in addressing the problem, too much emphasis has been placed on philosophical matters. Instead, the problem should be conceived as primarily a scientific problem, to be tackled by means of empirical investigation. At the root of Hey's position lies the observation that

> "[t]he species problem is caused by two conflicting motivations: the drive to devise and deploy categories, and the more modern wish to recognize and understand evolutionary groups" (Hey, 2001a: 329; Hey, 2001b: 105-110).

According to Hey, the first motivation cannot be realized in any nonarbitrary way. That is, attempts to devise categories that can be used to order organismal diversity will not generally result in natural categories, i.e., categories that exist independently of the context of human investigation. Primacy, in Hey's view, should therefore be placed on the latter motivation, i.e., the study of the units that feature in evolution. And this is in the first place a task for empirical science.

Contradicting Hey's suggestion, Pigliucci (2003) has recently argued that the species problem cannot be solved by empirical investigation alone:

> "the species problem has not gone away for the all-important reason that it is not the sort of empirical problem that can be solved by biologists alone. (…) it is a prime example of a philosophical question that requires input from empirical science (…)" (p. 599).

This view of the problem has also been taken by other participants in the discussions on the topic. In a classic paper from 1974, for example, the biologist Ghiselin stated that

> "[t]he species problem has to do with biology, but is fundamentally a philosophical problem (…) [W]e should note that we often fail to solve our problems because we cannot even identify them. Under such circumstances, conceptual investigations do more than just help. They are the only way out." (1974: 541 & 543).

If Pigliucci's and Ghiselin's assertions are correct (and I think they are), this brings about some interesting issues regarding the division of labor between philosophy of science and science itself. For one, it would be desirable to specify which aspects of the species problem are to be addressed by means of philosophical inquiry and which aspects are more suitable to be addressed empirically. Another issue would be whether the philosophical and the empirical work on the problem can be conducted largely independently, or should be done in close cooperation between the two domains of investigation. These issues cannot be properly addressed here, but the history of the species problem indicates that the problem is a concern of both fields of investigation and that cooperation is a fruitful way to approach the issue (cf. Hull, 2002). The extensive crossovers that have happened between the two domains of investigation on the species problem have not only resulted in a large volume of literature on the topic, but also in a couple of new philosophical insights. One of these, generally considered a major breakthrough in philosophy of biology and endorsed today by many participants in the debate on the species problem, is, for instance, the thesis that species should be attributed the ontological status of individuals rather than classes (Ghiselin, 1966; 1974; Hull, 1976; 1978). Yet, this 'species-are-individuals' thesis has not been able to set the species debate to rest and has itself become a topic of discussion (for recent opposition against the species-are-individuals thesis, see for example Ruse, 1998). The same holds with respect to other important insights regarding the species problem, such as species pluralism (which is discussed later in this chapter). Notwithstanding the close cooperation between philosophy and science, the species problem still stands.

This indeed suggests that the philosophical aspects of the species problem constitute an important factor in the problem's persistence, making it a problem that cannot be solved by gathering more empirical data alone. There is, however, reason to suspect that the philosophical aspects of the problem (as well as its empirical aspects, for that matter), however difficult they may be to resolve, by themselves do not constitute the fundamental cause of the species problem's persistence but merely constitute the symptoms of an underlying causal factor (cf. Mayr, 1957: 10). This can be seen by considering the multitude of extant definitions of the notion of species (see Chapter 3),

many of which are applied regularly in empirical studies. The application of the different available definitions to a given group of organisms in many cases yields several incompatible groupings of these organisms into tentative species. All of these tentative species constitute useful groupings for scientific study, suggesting that they are associated with different scientific concepts. Moreover, investigators working in different domains of biological science often pose incompatible demands on the notion of species (Kornet, 1993; Hull, 1997), depending on the role of this notion in addressing the particular research questions at stake in their field of investigation. The diversity of available definitions of the notion of species reflects this diversity of demands. The suggestion that these different demands pertain to one single scientific concept – one all-purpose species concept – inevitably results in failure to achieve a final solution of the species question in the form of a unique definition of the concept of species (or at least a set of definitions containing a unique definition for each organism group). After all, any solution to the issue that meets some of the requirements placed on the notion of species will fail to meet other, incompatible ones. One way to resolve this predicament is by recognizing that, in different contexts of investigation, distinct concepts are at stake that however all are denoted with the term 'species'. This, then, is the underlying reason for the species problem's persistence. As a consequence, the empirical and philosophical questions that have been addressed extensively in the discussions on the species problem then also rise with respect to each of the involved concepts separately.

How did this situation come about? On several occasions in the developmental history of biological science, the term 'species' has taken on a new meaning. When the Modern Synthesis was created and the widely used *Biological Species Concept* introduced, for example, the meaning of 'species' changed from its traditional denotation of classes of organisms to denoting groups of reproductively connected populations. The old meaning of 'species' was however not abandoned completely and the two meanings continued to coexist and to be used in biological investigations (cf. Mayr, 1942: 108-111). As a consequence of several such changes in the meaning of 'species', biologists today use the same term to denote a number of distinct scientific concepts. I argue for this perspective on the species problem extensively in Chapter 3 (Reydon, 2005) and shall illustrate it only briefly here.

Examination of what biologists mean when they use the term 'species' shows the term to refer to four distinct kinds of things: units that participate as wholes in evolutionary processes (units of evolution), segments of phylogenetic trees (phylogenetic taxa, i.e., historical pattern segments), kinds of organisms, and kinds of populations. From an ontological point of view, units of evolution and phylogenetic taxa

both are individuals (although they are individuals of different kinds), whereas kinds of organisms and kinds of populations have the ontological status of classes. The differences between these four kinds of things become clearer when their material composition is considered. Units that participate as wholes in evolutionary processes must be composed of synchronously living organisms, whereas phylogenetic taxa encompass organisms from the present as well as from the near and the more distant past. In addition, kinds of organisms have individual organisms as their members, while kinds of populations have populations rather than organisms as their members. For further discussion, I refer to Chapter 3 (Reydon, 2005), where examples are given that show that all these four kinds of things are being referred to as 'species' in current biological discourse. (It is important to note here that, in my view, the different concepts at stake are not *species* concepts in the sense that they are interconnected concepts that can be subsumed under one overarching concept of species; they are independent scientific concepts that merely share the same name.)

If the perspective on the species problem sketched above is correct, this sheds new light on several issues that have been topics of debate in the context of the species problem. Important topics among these are species pluralism (see Chapter 3), the species-are-individuals thesis (see Chapter 3 and the Appendix) and the question of species as natural kinds (see Chapters 4 & 5). To illustrate this, I now turn to a recent attempt to resolve the species problem by understanding the notion of species as a family resemblance concept. Because this attempt fails to distinguish between the different concepts called 'species', I argue that it fails as a definitive solution to the species problem.

2.3. Species as a family resemblance concept

The notion of family resemblance concepts was introduced by the philosopher Wittgenstein in his *Philosophical Investigations* (1953). The classic example of a family resemblance concept is the concept of game. Although there is general agreement among the members of the language community in which the term 'game' is being used on which things are included in the category of games, it is not possible to identify any characteristics that all and only games have in common:

> "What is common to them all? (…) if you look at them you will not see something that is common to *all*, but similarities, relationships, and a whole

> series of them at that. (…) we see a complicated network of similarities overlapping and criss-crossing (…)." (Wittgenstein, 1953, sec. 66; cf. sec. 67).

In other words, games do not possess essential properties in the sense that they do not possess any properties that are both necessary and sufficient for a given phenomenon to be included in the category of games. Given the problems confronting classic essentialism regarding species taxa, it would seem a natural move to understand species taxa as family resemblance classes (cf. Hull, 2002; an early example is Beckner, 1959: 22-25 & 64ff.). Yet, in practical applications this approach is confronted with serious problems; the placement of species boundaries, for instance, seems to become too much a matter of subjective judgement rather than of finding the natural state of affairs (cf. Ruse, 1998).

In the above perspective, individual species taxa are understood as families in the Wittgensteinian sense. An alternative move is to understand not individual species taxa but the species category (i.e., the category containing all past, present and future species) as a family of natural entities. This move was recently suggested by Pigliucci (2003), thereby presenting a novel application of Wittgenstein's notion of family resemblance in the species debate (but Beckner, 1959: 64, and Van Valen, 1988: 53, seem to constitute precursors to this approach):

> "species is a family resemblance concept whose underpinning is to be found in a series of characteristics such as phylogenetic relationships, genetic similarity, reproductive compatibility and ecological characteristics. These traits take on more or less relevance depending on the specific group one is interested as a function of the particular biology of that group." (Pigliucci, 2003: 601).

This position acknowledges that various types of species exist in nature and that, when studying a particular group of organisms, we ought to focus on those features that are the most important with respect to the origin and maintenance of species in the case at hand. Next to rendering the use of the notion of species in research practice more adequate to the messiness of biological reality (Pigliucci, 2003: 601; Van Valen, 1988: 55), this perspective on the concept of species can according to Pigliucci also explain why biological science has been able to proceed successfully all this time without being bothered by the persistent unclarity regarding the nature of species. In the case of the

concept of game, for instance, the impossibility of defining precisely what a game is does not hamper our ability to speak meaningfully about games and to illustrate what we mean by giving examples of actual games (Wittgenstein, 1953, sec. 69 & 71). The same holds for the concept of species:

> "(…) as biologists we *teach* our students what species are by example (…) For our purposes as biologists, we can draw on one set of threads or another to work with particular species, depending on what taxonomic group we are considering." (Pigliucci, 2003: 600).

Thus, although there exists a single concept of species valid for the whole of biological science, it is associated with a category of very diverse species taxa and must consequently be defined differently in different domains of biodiversity and for different research purposes. But can this approach constitute a solution to the species problem?

2.4. Species pluralism and family resemblance concepts

Answering this question invokes the idea of species pluralism. Although Pigliucci (2003 and pers. comm.) rightly emphasizes that his approach is different from the various pluralist approaches that are already available in the literature, there seems to be an important similarity between these two types of approach that is fatal to both. To clarify this point, let us see how Pigliucci's position relates to the different forms of pluralism.

Notwithstanding their sometimes profound differences, the various pluralist positions regarding the notion of species that have been proposed can be classified into two overarching (but not sharply delimited) types (Mishler & Brandon, 1987; Williams, 1992; Reydon, 2005 – see Chapter 3 for more a extensive discussion). The more radical type of species pluralism holds that the species concept can be broken down into a number of – to some extent – independent subconcepts that can be applied to *the same* organisms depending on the question under consideration. Ereshefsky, for example, holds that

> "An organism may belong to two different types of species at the same time. For example, a single organism may belong to both an interbreeding species and a phylogenetic species even though those species are not fully co-extensive." (1998: 106).

This type of pluralism has also been prominently advocated by philosophers such as Dupré (1993) (although in later work Dupré took a less radical position; Dupré, 1999: 18) and Kitcher (1984). The other, less radical, type of species pluralism is purely definitional in nature; this form of pluralism is advocated by, among others, Mishler & Brandon:

> "a single, optimal general-purpose classification exists for each particular situation, but (…) the criteria applied in each situation may well be different." (1987: 403).

Here it is not the case that there are several distinct species concepts that can be applied to the same organisms depending on the research question at stake, but rather there are several different definitions of the concept of species that each apply to particular organism groups for all research questions that can be considered with respect to these groups. This less radical type of pluralism is only pluralist insofar as it allows the existence of different kinds of species; in holding that these different kinds of species exist in different regions of the organismal world and that every organism belongs to precisely one species, it is a monist rather than a pluralist position. (Ereshefsky, 1998, for example, places emphasis on this difference between his type of species pluralism and Mishler & Brandon's less radical type.)

The difference between the two types of pluralism may be illustrated as follows. From a radical pluralist perspective, when studying for example the cichlid fish in Lake Victoria we may choose the concept adequate to our investigatory purposes: a historical concept based on common descent when investigating the phylogenetic relations between the various groups present in the lake and a concept based on structural similarity when studying their functional morphology. (Note that although these concepts are to some extent independent, they are similar at a basic level in that they all are *species* concepts. One can be a pluralist, after all, only with respect to things that are at some level the same. Cf. Chapter 3.) From a less radical pluralist perspective, no such thing is allowed: one unique definition of the species concept applies to the Lake Victoria cichlids, but this may very well be a completely different definition from the one that applies to, say, the orchids in the forests of Java. Yet, all definitions are definitions of one concept, i.e., the species concept.

The position that the concept of species is a family resemblance concept is opposed to "[t]he pluralist suggestion (…) that there are equally legitimate, *conceptually*

independent, species concepts that can be used depending on the interest of the investigator." (Pigliucci, 2003: 601, original italics). Instead,

> "species represent one large cluster of natural entities, quite independently of the interests of human observers. This cluster, however, is a loose one, with its members connected by a dense series of threads, not all of which go through every single instantiation of the concept." (*ibid*.).

The species problem is thus seen as involving a single scientific concept. Since the members of the species category, i.e., all actual species taxa, are interconnected by a complex network of biological factors that hold between some but not all species taxa, the species issue is best approached on a case-by-case basis, focusing on those factors that are relevant in a particular case. While rejecting central parts of both types of species pluralism (i.e., the radical pluralist view that there exist several independent species concepts and the less radical pluralist view that the species concept is to be defined differently for different organism groups, with one definition per organism group), this position does retain other important pluralist aspects. Firstly, even though there is no property that all members of the species category have in common, they all are *species* in that they are considered instances of the same scientific concept. As species taxa, i.e., instances of the same concept, they occupy similar positions in biological theory. This corresponds to the basic assertion found (sometimes implicitly) in both the more radical and the less radical forms of species pluralism that, even though the species category consists of different kinds of things, it is still meaningful to retain the species category as a distinct scientific category (Kitcher, 1984; Mishler & Brandon, 1987; Dupré, 1993; 1999; Reydon, 2005; Chapter 3). Secondly, emphasis is being placed on the need for various operational definitions of the species concept, rather than a single one, due to the diversity of natural factors that play a role in the origin and maintenance of different actual species. This is illustrated by Pigliucci's (2003) suggestion that Templeton's (1989; Mayden, 1997) *Cohesion Species Concept* comes close to the idea that the concept of species is a family resemblance concept. Templeton defines species as "populations of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (Templeton, 1989: 12), while various such cohesion mechanisms can be identified in nature (Templeton, 1989, table 2). This yields a situation in which different operational definitions of the concept of species exist, focusing on different cohesion mechanisms. Depending on the research question at stake and the particular biology of the species taxon under study, different operational

definitions are to be used in different cases, although no single all-purpose definition exists in any case (Pigliucci, pers. comm.). While rejecting the idea of one all-purpose definition of species per organism group, the idea is retained that different operational definitions of the notion of species can be used that in the end all define *species*.

So, why does this approach fail as a definitive solution to the species problem? The main problem with species pluralism in any form is a clash with the practice of biological research. Several dozens of competing definitions of the concept of species are readily available in the literature. As said above, in many cases the application of different definitions to the same group of organisms leads to incompatible groupings of these organisms into species (see Ghiselin, 1997: 129-130; Hull, 1997; Pigliucci, 2003; Reydon, 2005; Chapter 3; but see Ruse, 1998, for a dissenting viewpoint). When adopting a form of radical pluralism, these diverse groupings of the same organisms into species are all considered legitimate and scientifically useful (be it perhaps in various degrees). But, then, why do all these various ways of clustering organisms yield *species*? Less radical forms of pluralism avoid this issue by identifying one particular way of clustering into species as the correct one for a given group of organisms. The problem now is not so much why all the various legitimate ways of clustering organisms yield species, but which of the various ways of clustering is the one correct way of obtaining species as they exist in nature in any given case. This problem cannot be resolved, because the various possible groupings of the same organisms stand at the focus of different contexts of biological research where they are seen as natural groups that legitimately stand at the focus of scientific study (see Reydon, 2005; Chapter 3, for further discussion). Although the position advocated by Pigliucci cannot be seen either as a form of radical pluralism or as a form of less radical pluralism in the sense discussed above (because of its rejection of the view that there is precisely one adequate definition of the notion of species per organism group – perhaps it should be considered a third form of species pluralism for this reason), it does face this latter problem. Central in his position is the assumption quoted above that "species represent one large cluster of natural entities, quite independently of the interests of human observers" (Pigliucci, 2003: 601). Given that the various species definitions available in the literature yield different clusterings of organisms when applied to the same group of organisms, the question is thus how to identify which definition gives us *the* natural clustering into species. (Note that on the view that the term 'species' denotes multiple concepts the above problems do not arise, for each grouping of organisms into tentative species can be understood as being associated with a different concept.)

2.5. Conclusion

It is certainly true that the species problem is "a paradigmatic example of a philosophical question that requires empirical information (provided by science) to be settled, not of a scientific problem with unwelcome philosophical characteristics." (Pigliucci, 2003: 596). But despite the large amount of work that has been done on both the empirical and the philosophical aspects of the problem, still no adequate solution to the problem has been found. In the above discussion, I have attempted to show that the reason for this failure to resolve the species problem has more to do with the historical development of biological science than with the philosophical nature of the problem: the term 'species' has come to denote a number of distinct scientific concepts that occupy different positions in the conceptual framework of biological science. From this perspective on the species problem it can be seen why the various forms of species pluralism, as well as the view of the notion of species as a family resemblance concept, cannot constitute good solutions to the problem. In addition, it provides a new starting point for further empirical and philosophical work on the species problem. A beginning with this work is made in the following chapters.

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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.

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> *"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

[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

[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).

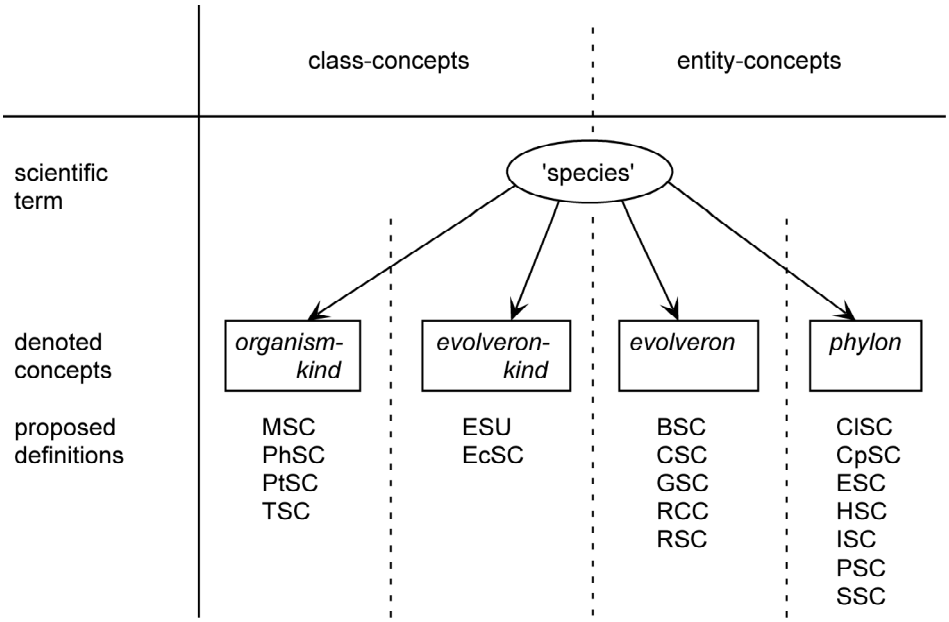

Figure 3.1: The term ‘species’ denotes four distinct scientific concepts. The most important definitions of ‘species’ are classified according to the concept to which they pertain. The following abbreviations are used: BSC = Biological Species Concept; ClSC = Cladistic Species Concept; CSC = Cohesion 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

[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 Roselló-Mora & Amann, 2001: 52-53; but see Roselló-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).

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[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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4 Generalizations and kinds in natural science: Why kind-generalizations and universality mismatch

Abstract

We argue that there is a hitherto overlooked distinction between two sorts of generalizations with explanatory and predictive force: generalizations over changes in states of affairs (*law-generalizations*) and generalizations over the member entities of kinds (*kind-generalizations*). While universality is an appropriate criterion for assessing putative law-generalizations, it does not match kind-generalizations. Furthermore, we argue that there are two sorts of kinds over which explanatory and predictive kind-generalizations hold: *causal kinds*, based on causal mechanisms, and *historical kinds*, based on shared history. We show that, contrary to the commonly held view, in biology not only historical kinds but also causal kinds constitute an important ground for explanation and prediction.

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4.1. Introduction

The central position of generalization in scientific explanation and prediction has long been recognized. As Reichenbach, for example, stated over half a century ago: "The essence of knowledge is *generalization*. (…) Generalization, therefore, is the origin of science." (1951: 5). The present chapter addresses the question which sorts of generalizations we need to make in order to explain and predict similarities in the properties of material entities.

The main claims that we argue for are the following. Firstly, there is a – hitherto overlooked – distinction between two different sorts of explanatory and predictive generalizations, which we call *law-generalizations* and *kind-generalizations*. Similarities in the properties of material entities are not explained and predicted by means of law-generalizations, but by means of kind-generalizations. Secondly, to explain and predict similarities in the properties of material entities two sorts of kind-generalizations are needed: generalizations over members of *causal kinds*, that is, spatiotemporally unlimited kinds of entities of which the similar properties are due to multiple instances of operation of the same causal mechanism(s), and generalizations over members of *historical kinds*, i.e, spatiotemporally limited kinds of entities of which the similarity is due to their shared history. Thirdly, while we endorse the view that the criterion of universality that is commonly used to assess the scientific validity of explanations and predictions is appropriate for explanations/predictions in terms of law-generalizations, we argue that it is misplaced for explanations/predictions in terms of kind-generalizations.

A question that we *do not* address in the present chapter is whether biology possesses laws, i.e., law-generalizations. Thus we do not discuss whether, say, the Hardy-Weinberg law, Mendel's laws of heredity, the laws of natural selection or the equations of Adaptive Dynamics (Metz *et al*., 1996) can be attributed the status of fundamental laws of nature. The question that we *do* address is which kind-generalizations are needed in science to explain and predict similarities in properties of material entities, i.e., which kind-generalizations are scientifically relevant. As stated above, we shall distinguish kind-generalizations that hold over two sorts of scientific kinds (which, it should be noted, we do not see as necessarily the two only sorts of scientific kinds). After having argued the difference between law-generalizations and kind-generalizations in Section 4.2, in Section 4.3 we shall discuss the scientific relevance of generalizations that hold over causal kinds. We shall show that generalizations that hold over causal kinds may be exceptionless as well as non-

exceptionless. In Section 4.4, we shall discuss the scientific relevance of generalizations that hold over historical kinds. We shall show that, similarly to generalizations holding over causal kinds, generalizations holding over historical kinds may be exceptionless as well as non-exceptionless. From this it follows that it is inappropriate to apply the criterion of universality to the notion of kind-generalization, in other words, that the notions of universality and kind-generalization mismatch.

4.2. The conflation of law-generalizations and kind-generalizations

The primary difference between law-generalizations and kind-generalizations lies in their material reference: law-generalizations do not directly refer to particular material entities, whereas kind-generalizations do. Law-generalizations are purely abstract generalizations that refer to the laws that govern the dynamics of nature. Law-generalizations thus explain and predict changes from states of affairs at time t_0 to states of affairs at time $t_1 > t_0$ (as, for example, the radioactive decay law $N(t)=N_0e^{-\lambda t}$) or state how dynamical parameters of material systems co-vary (as in Newton's law of gravitation $F=Gm_1m_2/r^2$).[15] In contrast, kind-generalizations such as 'All ravens are black' (to use a time-worn example) pertain not to changes in states of affairs but to the material entities that result from or take part in these changes. While scientific theories explain and predict what kinds of entities may exist (i.e., they map out the state space of stable states of matter), generalizations over the members of these kinds in turn explain and predict similarities in properties of their member entities on the basis of the factors underlying these kinds.[16] Note that while the existence of kinds of entities over which kind-generalizations hold can at least in part be explained by taking recourse to law-generalizations, this does not mean that the kind-generalizations themselves necessarily

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[15] For discussions of different types of laws of nature, see e.g. Cartwright (1983: 21-43, 100ff.), Cummins (1983: 6-7) and Weinert (1995: 4-14).

[16] Prima facie the law-generalizations/kind-generalizations dichotomy resembles the view defended by Cummins (1983: 1-22). According to Cummins, 'causal laws' (i.e., law-generalizations) explain changes in states of affairs, while properties of entities are explained in terms of underlying composition and organization. However, while Cummins addresses the issue what the possession of a property *P* by a system *S* consists in (1983: 15), we address the different question why it is that the same property *P* is being possessed by a number of separate natural entities (i.e., the members of a kind).

reduce to law-generalizations. Conversely, law-generalizations do not necessarily reduce to kind-generalizations: while for instance the law of gravitation describes the interaction between two massive objects, it does not describe any similarity between these entities (which indeed do not need to have any property in common).

In classic and contemporary accounts of scientific explanation and prediction, the distinction between law-generalizations and kind-generalizations is overlooked; both are subsumed under the notion of 'law' and all scientific explanation and prediction is considered to rest on such 'laws' (e.g., Reichenbach, 1951: 6; Cummins, 1983: v-vi). The 'laws', for instance, on which according to the deductive-nomological model all valid scientific explanations rest, encompass both law-generalizations and kind-generalizations (cf. Hempel and Oppenheim, 1948: 152-157; Hempel, 1965: 335-339; 488). Another example is Goodman's ([1954] 1973) account of predictive generalizations, in which the term 'law' is used to denote all predictive generalizations, including those that pertain to similarities exhibited by the members of a kind: according to Goodman ([1954] 1973: 21), "(…) rather than a sentence being used for prediction because it is a law, it is called a law because it is used for prediction (…)." This is a view that is still widespread today (see, for example, Mitchell, 2003: 142).

It is common practice in both classic and contemporary discussions to use universality as the principal criterion for assessing the validity of explanations and predictions and to evaluate the scientific status of disciplines – that is, their explanatory and predictive capacity – exclusively on the basis of whether their explanations and predictions rest on universal 'laws'. In the used notion of universality, the two notions of exceptionlessness and spatiotemporal unlimitedness are assumed to coincide:

> "[Universality] is standardly represented by the universal quantifier (x) in $(x)(Px \rightarrow Qx)$. The scope of the quantifier is taken to be all space and all time. (…) Once the scope of the law is understood as universal in this broadest sense, then it is clear that the truth of the law will permit no exceptions." (Mitchell, 2003: 131).

Correspondingly, the 'laws' on which all valid scientific explanations are supposed to rest are demanded to be exceptionlessly valid throughout all space and time. Application of the criterion of universality yields a picture in which scientific disciplines fall into either of two distinct domains (see Figure 4.1A on p. 75). Physics, then, is typically evaluated as the discipline of which the generalizations meet the criterion of

universality and biology as the discipline of which the generalizations are non-universal.[17]

A classic example both of the coupling of exceptionlessness and spatiotemporal unlimitedness under the notion of universality and of the use of universality as a criterion for evaluating the scientific status of disciplines is Smart's (1959; 1963) argument that biology is not an explanatory science. Smart argued that the biological sciences are of a different sort than the physical sciences because the latter possess "(…) laws [that] are universal in that it is supposed that they apply everywhere in space and time (…)", whereas the former only possess generalizations that explicitly or implicitly use proper names referring "our own particular station in space and time" (1959: 360, 362; cf. 1963: 53ff.). The names of species, Smart argued, make implicit references to the evolutionary tree of life on Earth, implying that no spatiotemporally unlimited truths can be formulated with respect to any particular species. According to Smart, redefining the names of species in such a way that they no longer possess a spatiotemporally limited referent cannot solve this problem because then the feature of non-exceptionlessness surfaces: "(…) if the propositions of biology are made universal in scope, then such laws are very likely not universally true" (1963: 54; cf. 1959: 361-362), that is, they are not exceptionless. For Smart, thus, universality consists in the conjunction of spatiotemporal unlimitedness and exceptionlesness. Smart (1959: 363-364; 1963: 57) concluded that because biological generalizations are not universal, they cannot be 'laws', and consequently biology cannot be understood as a science that possesses explanatory and predictive capacity of its own. Instead, biology is to be seen as more akin to technological disciplines.[18]

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[17] For a similar distinction, see McAllister (1997); for discussion, see also Rosenberg (1985: 219-225); Kornet (2002).

[18] Note that even when accepting Smart's premises, his conclusion is not unavoidable. Mayr, for instance, asserted: "Generalizations in biology tend to be statistical and probabilistic and often have numerous exceptions. Moreover, biological generalizations tend to apply to geographical or otherwise restricted domains" (1988: 19). Mayr, however, did not take this as indicating the inferiority of biology as a scientific discipline but rather as pointing to its autonomy. Recently, Mitchell asserted that "[t]he failure of knowledge claims in biology or other sciences to live up to the universal, exceptionless character of the ideal case does not preclude their functioning as "laws", generalizations that ground and inform expectations in a variety of contexts." (2003: 146), thus stretching the meaning of 'law'. Cf. the discussion in Mitchell (2003: 138-148).

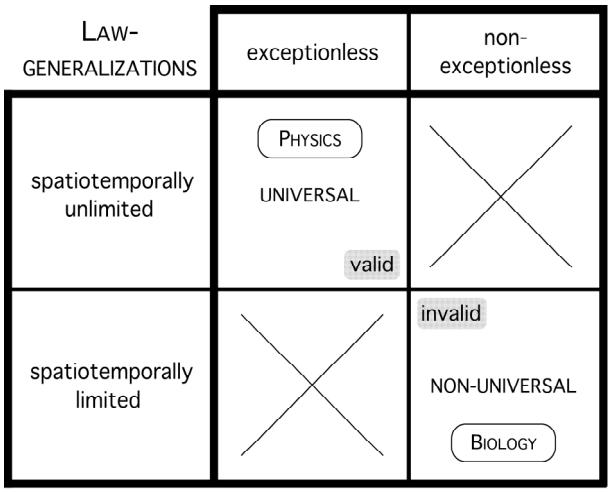

Figure 1A

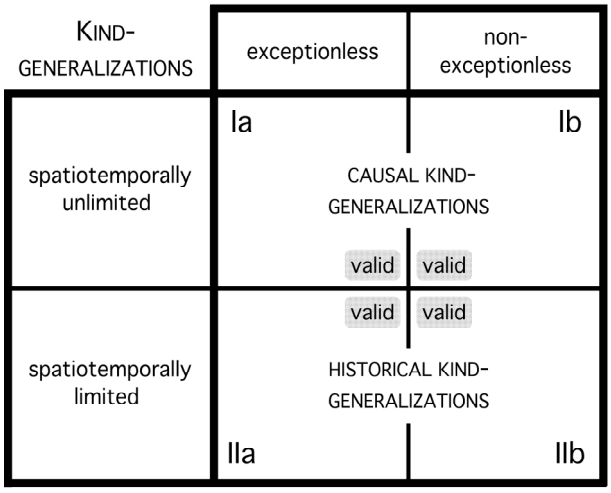

Figure 1B

Figure 4.1. A. The common picture of scientific disciplines falling into two domains, according to the criterion of universality. The universal generalizations of physics are considered scientifically valid law-generalizations, in contrast to the non-universal generalizations of biology. B. The mismatch of kind-generalizations and universality. There are two sorts of scientifically valid kind-generalizations: over the members of causal kinds (box I) and over the members of historical kinds (box II). Both sorts of kind-generalizations can be exceptionless (boxes Ia and IIa) or non-exceptionless (boxes Ib and IIb).

Similar arguments have been put forward more recently by Hull (1978: 353-354) and Rosenberg (1985: 204-212; 2001), who also (tacitly) couple exceptionlessness and spatiotemporal unlimitedness under the notion of universality and apply the criterion of universality to biological generalizations regarding species. Hull and Rosenberg argue that these generalizations are not universal, hence are not 'laws' and therefore do not contribute to scientific explanation. While Hull (1978: 353) leaves open the possibility to find biological 'laws' elsewhere, Rosenberg (1985: 219-225; 2001: 737-742) reaches a conclusion similarly to Smart's, i.e., that biology is a discipline that operates in a 'nomological vacuum' and is concerned with individual case studies rather than with uncovering explanatory and predictive 'laws'.

What in our view is wrong in the classical and contemporary accounts of explanation and prediction as well as in Smart's, Hull's and Rosenberg's arguments, is the conflation of law-generalizations and kind-generalizations under the notion of 'law' and the consequent (and unwarranted) a priori rejection of generalizations that do not meet the requirement of universality as not relevant in scientific explanation and prediction. The kind-generalizations that we discuss in the remainder of this chapter constitute a case in point.

4.3. Generalizations over causal kinds

In this section, we show the scientific relevance of kind-generalizations holding over causal kinds (this is illustrated by box I in Figure 4.1B). Causal kinds are kinds of material entities that exhibit similar properties because of their being subject to the same causal mechanism(s). Natural kinds, as traditionally conceptualized, are those causal kinds that rest on the causal mechanisms that maintain the stable existence of the member entities of the kinds in question. As we shall argue, generalizations that hold over causal kinds are spatiotemporally unlimited but may be exceptionless (box Ia) or non-exceptionless (box Ib) (Section 4.3.2). Furthermore (Section 4.3.3), we demonstrate that generalizations over causal kinds are necessary in biological science to explain and predict some organismal similarities that are present in nature. This shows that it is incorrect to allocate biology to the domain of disciplines of which the generalizations are typically non-universal and hence non-explanatory (the lower right box in Figure 4.1A), as Smart, Hull and Rosenberg do.

4.3.1. The scientific relevance of generalizations over causal kinds (box I)

According to the traditional view, tracing back to the by now classic 'new theory of reference' developed by Kripke and Putnam, scientific investigation is essentially concerned with "(…) *natural kinds* – that is, with classes of things that we regard as of explanatory importance; classes whose normal distinguishing characteristics are 'held together' or even explained by deep-lying mechanisms." (Putnam, [1970] 1977: 102; original italics; cf. 1983: 71-74; Quine, 1969: 21). Physical and chemical kinds, such as the kinds of elementary particles and the chemical elements, are standardly quoted as examples of natural kinds. One central aim of scientific investigation, then, is the explanation of the similarities between members of the same natural kind by reducing these to the factors that underlie the generalizations over this kind (Quine (1969: 22), for example, took success in performing such explanatory reductions as the hallmark of any mature science).

Although philosophical accounts commonly render the Kripke-Putnam theory as conceptualizing natural kinds in terms of microstructural essences, the explanatory core of the theory is formed by causal mechanisms rather than microstructural essences. (A similar point was made by Sober (1980: 354) with respect to the putative essences of species in biology.) According to Putnam, microstructural composition, in those cases in which it is an important explanatory factor, does not constitute the *principal* explanatory factor:

> "To belong to a natural kind, something must have the same composition, or obey the same laws – indeed, what makes composition important, *when* it is, is its connection with laws of behavior – as model members of the class (…)" (1983: 74, our italics; cf. [1970] 1977: 102).

Atomic number and microcomposition, to name two standard examples of kind essences, by themselves do not explain or predict much. The similarities in structural and behavioral properties of, say, ^{56}Fe-atoms are not in the first place explained and predicted by their having atomic number 26 or, more precisely, microcomposition of 26 protons, 30 neutrons and 26 electrons. The explanatory and predictive force of atomic number and microcomposition is *derived* from the causal mechanisms incorporated in atomic theory. What renders microcomposition explanatorily important is its role as one of the initial conditions on which these causal mechanisms operate, allowing systems of 26 protons, 30 neutrons and 26 electrons to stably persist in particular circumstances.

Explanatory and predictive force lies foremost in the generalizations that rest on these causal mechanisms (Putnam's "deep-lying mechanisms"), rather than with parameters such as atomic number, microcomposition, etc., that enter into these generalizations.

Under the Kripke-Putnam theory, what are considered to be the kind essences of natural kinds thus is dependent on the causal basis on which the – at any time accepted – scientific theories explain and predict the similarities of the member entities of the same kind. While Putnam asserted that "[w]hat makes something gold is having the same nature as the paradigms; in current physical theory this is unpacked as having the same composition (…)" (1983: 73), he acknowledged that the way in which the nature of gold is unpacked in scientific theory could have been otherwise:

> "[W]hat sharing a nature is, is determined by our evolving theories (…) of the several sorts of natural kinds, and not *a priori*." (1983: 73, original italics);

and:

> "What the essential nature is is not a matter of language analysis but of scientific theory construction; *today* we would say it was chromosome structure, in the case of lemons, and being a proton donor, in the case of acids." ([1970] 1977: 104, emphasis added).

This is however not to say that according to Putnam kind essences *themselves* are dependent on which scientific theories are accepted at a particular time. Rather, kind essences are unchanging, fixed by the world (Putnam, 1983: 71), and can be correctly or incorrectly identified in scientific investigations. (This is why, in the Kripke-Putnam theory, scientific kind names are rigid designators.) Scientific progress, then, (in part) consists in the correct identification of kind essences (cf. Quine, 1969: 22; Putnam, 1983: 71). That today we no longer consider sharing a particular genetic structure as essential for organisms of the same kind, illustrates this progress in theory development.

Generalizations that explain and predict similarities in properties of material entities on the basis of causal mechanisms can however be made not only over the members of traditionally recognized natural kinds, but over material entities of any kind that exhibit at least one similar structural or behavioral property as a result of the

operation of the same causal mechanism(s) on similar subject matter.[19] We reserve the term 'natural kind' for the most fundamental causal kinds in the sense of those causal kinds for which the underlying factor consists in the causal mechanism(s) that maintain the stable existence of their member entities; our category of causal kinds thus includes the category of natural kinds as a subcategory.[20]

The causal mechanisms that underlie causal kinds are ultimately rooted in fundamental laws of nature and thus will cause multiple independent instantiations of entities of the same kind at any location or time, given that the right conditions obtain. This means that causal kinds and the generalizations that hold over them are intrinsically spatiotemporally unlimited, that is, the members of causal kinds may *in principle* occur at any spatiotemporal location. However, causal kind-generalizations themselves are not law-generalizations: they do not generalize over changes in states of affairs (as law-generalizations do), but over members of kinds. Although causal kind-generalizations are founded on causal mechanisms that in turn rest on laws of nature, they themselves do not describe the mechanisms and underlying laws on which they ultimately rest (this is the task of law-generalizations). While scientific theories and the causal mechanisms that they incorporate define the state space of all possible stable structures of matter, that is, all causal kinds of possible entities (cf. Rosenberg, 1985: 202; Mahner & Bunge, 1997: 16-17; 221-222), the generalizations that hold over these kinds, in turn, explain and predict the similarities of the members entities of a kind. In the case of fundamental natural kinds such as the chemical elements, for instance, atomic theory accounts for the design space of all possible stable atomic structures, i.e., the Periodic Table. The causal mechanisms accounted for by atomic theory, in combination with the applicable initial conditions, underlie the kind-generalizations that explain and predict the similarities exhibited by entities of the same instantiated isotope (such as ^{56}Fe) as well as kind-

[19] This in contradistinction to the widely held view that always *multiple* explanatorily relevant generalizations should hold over any 'good' scientific kind; Millikan for example asserted: "A science begins only when, at minimum, a number of generalizations can be made over instances of a single kind (…)." (1999a: 48; cf. 2000: 25).

[20] A somewhat similar view has been advanced by Mahner & Bunge (1997: 218-222), who distinguished between natural kinds *sensu lato*, i.e., kinds of entities that are similar with respect to some properties that are explained by causal generalizations, and natural kinds *sensu stricto*, that is, kinds of entities that are similar with respect to the maximum number of such properties.

generalizations that hold over as yet uninstantiated isotopes (such as the nowadays increasingly realized isotopes with atomic number >100).

Contrary to the common view, explanations in terms of causal kinds and the design spaces (i.e., spaces of possible organismal structures) that contain them are also important in biology. Thus, we argue in Section 4.3.3, biology is incorrectly allocated to the domain of disciplines that possess only non-universal and thus non-explanatory generalizations. (A biological example discussed there concerns the design space of possible skeleton structures of Burgess Shale animals).

4.3.2. Generalizations over causal kinds need not be exceptionless (box Ib)

Putnam ([1970] 1977: 103) pointed out that many natural kinds allow the existence of member entities that exhibit exceptional properties (in his terminology 'abnormal' members) and, in addition, that over time changes may occur in the set of properties that characterize the majority of kind members as environmental circumstances change (Putnam, [1970] 1977: 106; cf. the discussion of essentialism by Sober, 1980: 355-356). To consider causal mechanisms rather than microcomposition as the explanatory factors that underlie causal kinds, allows us to understand the existence of exceptions to the rule as well as changes in the set of properties that characterize kind members in a particular timeslice.

While Kripke and Putnam did not further elaborate the notion of causal mechanisms as the 'essences' of scientific kinds, Boyd (1989; 1991; 1999a; 1999b; 2000; Keller *et al.*, 2003) proposed a philosophical theory of scientific kinds in terms of causal mechanisms that explicitly accounts for the explanatory relevance of non-exceptionless generalizations over kinds of entities. The causal kinds based on these causal mechanisms ('homeostatic property cluster kinds' based on 'causal homeostatic mechanisms', in Boyd's terminology) are kinds of systems that are defined by the family *F* of properties that repeatedly co-occur in their member entities and the collection of causal mechanisms responsible for this repeated co-occurrence (Boyd, 1989: 16-17; 1991: 141; 1999a: 143-144; 2000: 67). Since the similarities of the entities of a scientific kind rest on causal mechanisms rather than on properties that are necessary and sufficient for kind membership (as is the case in micro-essentialist theories of natural kinds), imperfections in similarity do not imply exclusion from the kind in question. According to Boyd, an entity may lack one or more of the properties in *F* or may be unaffected by some of the associated causal mechanisms, while still belonging to the scientific kind in question (Boyd, 1999a: 143; 2000: 67; Keller *et al.*, 2003: 105).

Furthermore, the property family *F* defining a scientific kind is not necessarily unchanging in Boyd's view. As time proceeds, new properties may become included in *F* and old properties may become excluded.

The central question that however neither Putnam nor Boyd answer is how exceptions *actually* come about. We identify two reasons: the causal mechanisms that underlie causal kinds and the generalizations that hold over them (1) are usually governed by multiple fundamental laws and (2) in many cases operate on similar but non-identical entities.

The first reason for the existence of exceptions in generalizations over the members of causal kinds is implied in Cartwright's (1983) argument that the 'laws'[21] of physics do not explain changes in states of affairs in the real world. Cartwright argues as follows. The fundamental 'laws' that are used in explanations in physics are ceteris paribus generalizations, that is, they can only correctly explain changes in states of affairs in special cases – those cases in which they are invoked individually and particular ideal conditions obtain (1983: 45-47). In reality, however, it virtually never is the case that just one single 'law' applies. In real cases, multiple 'laws' are conjointly involved in determining changes in states of affairs. According to Cartwright (1983: 11ff., 56-59, 72-73), this means that explanations of real changes in states of affairs are always based on what she calls 'composition of causes': the generalizations that explain and predict real changes in states of affairs ('phenomenological laws' – Cartwright, 1983: 13-15, 100-127) rest on conjunctions of fundamental 'laws'. The 'laws' involved in any particular case make up a part of each other's boundary conditions and will often cause the applicable ceteris paribus clauses to be violated. In many cases, thus, the fundamental 'laws' do not correctly describe the case at hand, meaning that the fundamental 'laws' of physics are not generally exceptionless (Cartwright, 1983: 46ff., 54).

Although Cartwright formulated her argument with respect to the 'laws' in physics, we believe it applies as well to explanatory and predictive kind-generalizations over causal kinds in all scientific disciplines in which these occur. Consider the following example from biology (which we consider more extensively in Section 4.3.3). Many (but not all) free-swimming fish and all organisms in the mammalian order Cetacea (dolphins, porpoises and whales) possess streamlined fusiform body shapes. This similarity is explained by means of invoking hydrodynamic generalizations that rest

[21] The laws that Cartwright considers implicitly encompass both law-generalizations and kind-generalizations.

on a combination of fundamental laws regarding friction, pressure, acceleration and lift, that operate in the context of an evolutionary mechanism. The principal factor underlying the occurrence of streamlined body shapes is the reduction of pressure drag for motion in water (Thompson, 1942: 965-966; Webb, 1988; McGowan, 1999: 199-200 & 254-255). This explanation however does not imply that all members of the kind 'aquatic organisms', which is the causal kind encompassing all organisms that are subject to these hydrodynamic generalizations, necessarily exhibit streamlined fusiform body shapes. For small and/or slowly swimming organisms pressure drag becomes less important than other factors in aquatic motion (Webb, 1988: 718; McGowan, 1999: 197-199), so that the hydrodynamic laws regarding pressure drag reduction are easily overruled by other laws, resulting in non-fusiform body shapes. But also for larger organisms for which pressure drag does constitute an important factor, the hydrodynamic laws regarding pressure drag reduction can be overruled by other more important factors. Rays and skates (Batoidea), for example, are comparatively large free-swimming fish that spend much time on the sea floor. As a consequence, they do not possess fusiform bodies because in their case ground contact forces have overruled the pressure drag law (cf. Webb, 1998: 712).

In many cases causal mechanisms operate on entities that are similar without being identical; this constitutes a second reason to expect exceptions. Organisms of the same causal kind, for example, generally exhibit a high degree of variation in genetic makeup. This means that even when only one single natural law would operate on organisms of the same causal kind, the outcomes would still be variable. In the above example, because of their genetic differences no two cetaceans will possess perfectly identical body shapes, although all will possess fusiform bodies. Note that this is not an idiosyncracy of living nature: structural differences also exist between different actual ^{56}Fe-atoms (for example with respect to the energy levels of the electrons), so that different ^{56}Fe-atoms will exhibit to some extent different properties.

While the fundamental laws of nature themselves that underlie causal mechanisms are indeed exceptionless, the kind-generalizations over causal kinds that are based on such mechanisms thus need not be exceptionless. Because generalizations over spatiotemporally unlimited causal kinds need not be exceptionless, the notion of universality as discussed in Section 4.2 does not apply to generalizations over causal kinds.

4.3.3. Causal kinds in biology

The common view that biology does not possess explanatory and predictive generalizations (as represented in Figure 4.1A) is contradicted by the existence of a long-standing, though far from generally acknowledged, tradition in biological science of recognizing causal kinds as the bases for explanatory and predictive generalizations regarding some organismal similarities. This tradition centers round the notion of organismal design.

Consider, as an example of how design principles are applied in explanations and predictions of organismal similarities, the similarity mentioned above between cetaceans and fish with respect to streamlined fusiform body shapes. This similarity cannot be explained by historical factors, because the developmental pathways for the formation of a fusiform body are different for the two organism groups and have arisen independently in evolutionary history on the basis of different genetic makeups (Raff, 1996: 49, 388, 400-404). The fusiform body shape of cetaceans is due to the evolution of a novel developmental pathway in their ancestral population after its organisms had returned from living on land to living in aquatic environments, rather than to old developmental pathways that "(…) were saved for a rainy day through more than 300 million years of terrestrial evolution." (Raff, 1996: 388). As we described above, rather than by means of a historical generalization, the similar fusiform body shape of cetaceans and free-swimming fish is explained by means of causal generalizations grounded in hydrodynamic laws. This explanation works in a similar manner as the explanation of the similar properties of ^{56}Fe-atoms: the invoked law-based causal generalizations explain the multiple instantiations of the same property in organisms that belong to independent populations that lack any (with respect to the trait in question, that is) relevant historical connection. Moreover, the causal generalizations allow the prediction that future organisms that move freely in water will also possess fusiform streamlined bodies, irrespective of their ancestry.

D'Arcy Thompson (1942: 965-966) already observed that the hydrodynamic principles that account for the streamlined shape of plastic bodies immersed in streaming fluids (Thompson's example concerned a drop of mercury immersed in an airstream) should also somehow be invoked in the explanation of the streamlined body shapes of organisms. However, for Thompson it remained elusive how these principles could be used to account for streamlined body shape as a *heritable* organismal trait:

> "[T]he stream will tend to impress its stream-lines on the plastic body, causing it to yield (…) until it ends by offering a minimum of resistance (…). [A]nd the same principle must somehow come into play (…) in the making of a fish or of a bird. But it is obvious in both of these that (…) it is also an inheritance of the race; and the twofold problem of accumulated inheritance, and of perfect structural adaptation, confronts us once again and passes all our understanding." (Thompson, 1942: 965-966).

Thompson's problem is resolved by realizing that unlike the case of ^{56}Fe-atoms and drops of mercury, the causal factors in this case do not operate directly on individual entities to induce a fusiform body shape. The biological explanation of the fact that all cetaceans and many free-swimming fish possess fusiform bodies rests on the operation of the causal factors on the population level, defining one of the stable organismal states that is adapted to life in water (i.e., one of the feasible options in organismal design space) to which the two ancestor populations of cetaceans and fish evolutionarily converged. The causal kind based on these causal factors is a 'genuine' scientific kind (*sensu* Goodman, [1954] 1973: 122-123): the kind-generalization that holds over it explains why organisms of this kind possess fusiform bodies and why the same body shape has repeatedly evolved as a consequence of the limited number of options allowed by the laws of hydrodynamics. Moreover, it also reliably (but not unfailingly) predicts that *if* an unobserved present or future organism would belong to the kind in question (i.e., would fall under the involved hydrodynamic laws), it would possess a fusiform body.

Wouters (1999; 2005) recently provided a philosophical account of how design principles are able to ground biological explanations. According to Wouters, 'design explanations' explain organismal properties by referring to the requirements of maintaining an organism's living state and invoking projectible causal generalizations to account for (1) why organisms need (or why it would be beneficial) to exhibit a particular property in particular circumstances and (2) why this property has the form that it has (Wouters, 1999: 221-237, 263; 2005: 37). In biological explanations of organismal properties and similarities both design explanations and historical factors are invoked, design explanations accounting for "(…) *what would be useful* to the organism in certain circumstances", while "[e]volutionary reasons concern *what actually happened* in the past." (Wouters, 2005: 59; original italics).

That design spaces are indeed indispensable in explaining and predicting some organismal similarities that are found in nature is seen from the following case. Griffiths

(1996) argued that for design principles to be explanatorily important, most regions in design space should in fact be occupied at some point in evolutionary history, because only then

> "[t]he particular historical pathway by which a viable region was reached does not satisfyingly explain why organisms are found in that region rather than some other, because almost all viable regions were reached by some organism." (1996: S7).

Griffiths (1996: S7) used the Cambrian explosion as a counterexample to show that design principles are not explanatory:

> "(…) the diversity of the fauna produced in the Cambrian explosion suggests that the space of biological possibility contains many more discrete regions of viable form than have actually been explored."

Recent research from the domain of theoretical morphology, in which (in this case macromorphological) design spaces and underlying design principles are commonly invoked as the bases of explanation and prediction of organismal similarities (McGhee, 1999: 10-33), contradicts Griffith's conclusion and thereby shows the importance of design explanations in biology. This example concerns the skeletal structure of Burgess Shale animals (Thomas *et al.*, 2000). By constructing a 'Skeleton Space', consisting of a limited number of viable design options for animal skeletons (Thomas *et al.*, 2000: 1239-1240; cf. McGhee, 1999: 29-32), the researchers were able to explain the diversity of skeleton structures found in Burgess Shale animals as those structures that were to be expected on the basis of generalizations over Skeleton Space. The researchers found that the largest part of Skeleton Space was rapidly explored during Burgess Shale evolution and concluded that this "(…) confirms that evolution follows rational and consequently predictable patterns (…)" (Thomas *et al.*, 2000: 1242).

At present several types of research programs exist that use design explanations, focusing on different sorts of organismal properties. One type of program focuses on organismal macrostructure; examples are theoretical morphology discussed above and process structuralism (e.g., Goodwin, [1994] 2001). A different type of program focuses on organismal microstructure, studying organisms as metabolic systems. Examples are Kauffman's (1993) program and the emerging field of systems biology that particularly clearly exhibits an emphasis on prediction in its aim to discover

"[s]trategies to modify and *construct* biological systems (…) based on definite design principles (…)" (Kitano, 2002: 1662; emphasis added). A third, very different, type of programs use mathematical laws to explain and predict general patterns that are found in both living and non-living nature (e.g., Stewart, 1998; Ball, 1999).

The necessity of design explanations in some biological explanations implies, again, that biology cannot be allocated to the domain of disciplines that do not possess and explanatory generalizations of their own (cf. Kornet, 2002: 60-61).

4.4. Generalizations over historical kinds

There is no a priori reason why only generalizations that hold over spatiotemporally unlimited causal kinds should possess scientific value. As we show in this section, next to causal kinds that rest on causal mechanisms, there is at least one other type of kinds that underlie explanation and prediction: historical kinds that rest on historical factors (this is illustrated by box II in Figure 4.1B).[22] In Section 4.4.2, we show that historical kinds may be exceptionless (box IIa) as well as non-exceptionless (box IIb). In Section 4.4.3, we show how causal kinds and historical kinds are commonly confused in the recent literature.

4.4.1. The scientific relevance of generalizations over historical kinds (box II)

The presence of a particular property or set of properties in the member entities of historical kinds is due to their possessing a common history in which this property or set of properties has arisen at a particular spatiotemporal location. Like causal kinds, historical kinds rest on natural factors that are primarily (though not necessarily exclusively) responsible for the similarities that their member entities exhibit, so that generalizations can be made over them that explain observed similarities and predict as yet unobserved present and future instances.

That causal and historical kinds indeed constitute two distinct types of scientific kinds is seen from their spatiotemporal extent. Contrary to causal kinds, historical kinds are inherently spatiotemporally limited because of their foundation on particular

[22] Others who have pointed to the notion of historical kinds include Millikan (1998: 56-58; 1999a; 2000: 18-23); Boyd (1999a; 1999b) and Griffiths (1999).

historical events. Only entities that stand in the appropriate historical relation to the other members of a particular historical kind also count as members of this kind.

Whether in a particular case there is a historical kind of entities over which explanatory and predictive generalizations hold, depends on the nature of the processes involved. As Sober (1988: 3-5) pointed out, the possibility of *retrodicting* past from present events and states of affairs essentially depends on whether the processes that connect past, present and future are information preserving or information destroying. Processes that yield the same final state regardless of the initial state are highly information destroying and thus do not allow to retrodict the initial state from the final state (equilibrating processes are examples; Sober, 1988: 3). Processes that yield very different final states on the basis of slightly different initial states are highly information preserving and hence allow such retrodiction. With respect to historical kinds, not just the possibility of retrodiction but also of explanation and prediction is at stake. For a historical kind of entities, over which explanatory and predictive generalizations hold, to be present in a given case, at least one of the processes involved must preserve information regarding the properties of earlier entities in the properties of later entities. As Sober (1988: 5) emphasized, it is an empirical matter whether a process under consideration is information preserving or destroying. Thus, whether in a particular case the similarities of particular entities can be explained and predicted by means of generalizations over a historical kind is not a priori decidable, but depends on whether the process(es) at work preserve(s) information regarding the properties of the entities in question. In principle, historical kinds should play an important explanatory and predictive role in any scientific discipline that is concerned with processes that preserve information regarding the properties of previous entities in the properties of later entities.

The best-known examples of historical kinds, over which explanatory and predictive generalizations hold, occur in biology. In contrast to the physical and chemical sciences, the biological disciplines commonly take historical factors as most important in explaining the similarities between the entities under study. Mayr & Bock, for example, recognize that organismal similarities can be due to various types of factors, but assert:

> "[T]he important similarity for biological classification is ancestral similarity that provides the definition for the concept of homology (…). For biological classification, the correct formal statement is that entities are grouped together as members of a taxon because they share a suite of homologous features (…). Homologous features are those features in

> different organisms that are derived phylogenetically from the same feature in the immediate common ancestor (…)." (Mayr & Bock, 2002: 178).

Because evolution in many cases preserves information regarding ancestral organismal states, historical kinds of organisms exist over which generalizations can be made that explain and predict organismal similarities (cf. Mayr,1981; Mayr & Bock, 2002: 172, 186). This however does not mean that historical kinds are all-important in explaining and predicting organismal similarities: as shown in Section 4.3.3, some organismal similarities (i.e., typical instances of convergent evolution) require explanations in terms of causal rather than historical factors.

As an example, consider again a similarity between fish and cetaceans, this time with respect to the trait of possessing a backbone. The biological explanation of the fact that all cetaceans and all fish possess backbones indeed rests on a historical factor, i.e., the fixation at a particular point in space and time of the trait of possessing a backbone in the ancestral population of the clade (monophyletic group of species) Vertebrata, the historical kind to which both cetaceans and fish belong. (Correspondingly, in phylogenetic systematics the clade Vertebrata is supported by one synapomorphy, i.e., the character state of possessing a backbone.) This historical kind is a 'genuine' scientific kind (*sensu* Goodman, [1954] 1973: 122-123): the historical generalization that holds over it, based on the historical factor in question, explains why organisms of this kind possesses a backbone and reliably (but not necessary unfailingly) predicts that *if* an unobserved present or future organism would belong to the kind, it would possess a backbone.

Note that although for the trait of possessing a backbone to remain present in the clade Vertebrata the developmental pathway for the formation of a backbone must be entrenched in organismal development, this does not *by necessity* imply its linkage to *other* properties exhibited by members of the clade Vertebrata. Although in most cases there will exist such a linkage, implying that for most biological historical kinds multiple generalizations will hold over the same historical kind, it is an empirical matter whether this will always be the case. This, however, does not diminish the scientific relevance of historical kinds (as Millikan, 1999a: 56, for instance suggests): even in cases in which only one single generalization can be made over a particular kind, this generalization still explains and predicts the similarity of the kind's member entities in one particular respect (see also Section 4.3.1 and note 19).

4.4.2. Generalizations over historical kinds need not be non-exceptionless (box IIa)

As discussed above, the explanatory and predictive force of generalizations over historical kinds is dependent on the extent to which the processes that are at work to connect past, present and future preserve information regarding earlier organismal properties. The strength of information preservation may vary between processes and there is no a priori reason why a process cannot be fully information preserving. Although in many cases generalizations over historical kinds will exhibit exceptions, they can thus also in principle be exceptionless.

In biology, different degrees of information preservation can be seen for different organism groups. Organisms that belong to the same segment of the tree of life come into being on the basis of gametes that are copied from ancestor organisms and develop under similar environmental circumstances as their ancestors, thus rendering phylogenetic tree-segments candidate historical kinds (Millikan, 1999a: 55; 2000: 19-20; cf. also Griffiths, 1997: 211-213; 1999, and Chapter 5). Since spontaneous mutations and changes in environmental circumstances, among other factors, can induce the evolutionary loss of a particular organismal property in any given part of the tree of life, tree-segments as historical kinds in general are not exceptionless. Cichlid fish in African lakes, for instance, are renowned for exhibiting extremely rapid evolutionary change (e.g., Galis & Metz, 1998). In this case the reproduction process linking past to present and future weakly preserves information regarding ancestral organismal properties. In contrast, in the case of organism groups that hardly exhibit evolutionary change – 'living fossils' such as coelacanths and horseshoe crabs are well-known examples – the copying process is highly information preserving, making generalizations over these historical kinds possible with a very low degree of exceptions. Generalizations over historical kinds with a low degree of exceptions (in principle up to zero) are not only possible for 'living fossils', but also for evolving groups. The clade Vertebrata is an obvious example, all members of which possess backbones.

We conclude that because historical generalizations over spatiotemporally limited historical kinds may in principle be exceptionless as well as non-exceptionless, the notion of universality does not apply to generalizations over historical kinds.

4.4.3. Historical kinds do not constitute a subcategory of causal kinds

We have introduced the category of historical kinds as a separate category of scientific kinds over which explanatory and predictive generalizations can be made, next to the

category of causal kinds. Although some authors have recognized the scientific importance of generalizations over the members of historical kinds, it is not generally recognized that the kinds over which historical generalizations hold are essentially of a different sort than those over which causal generalizations hold. Here we examine the positions that have recently been advanced by Millikan (1999a; 1999b; 2000) and Waters (1998) and show that they incorrectly conflate causal and historical kinds.

Millikan (1999a: 50-53; 1999b: 100-101; 2000: 18-23) makes a distinction between two mutually exclusive types of scientific kinds, 'eternal kinds' and 'historical kinds'. However, Millikan holds that both types of kinds can be accounted for by Boyd's theory of kinds (see Section 4.3.2) and correspondingly considers the two types of kinds as subcategories of an overarching ontological category of 'real kinds' (1998: 57-58; 1999a: 53ff.; 2000: 18-23). (Millikan uses 'natural kinds', 'real kinds' and 'substance kinds' interchangeably and asserts that "[a] kind is a natural kind when there is a univocal principle (…) that explains for each pair of members, why they are alike in a number of respects" (1999b: 100; cf. 1998: 57-58).) A similar view is taken by Griffiths (1996: S5; 1997: 188-190, 212-213; 1999: 215-219) and by Boyd (1999a: 154-156; 2000; Keller *et al*., 2003: 105) himself.[23]

However, in our view it is incorrect to subsume historical kinds under Boyd's account. According to Boyd (1999a: 143; 2000: 67; Keller *et al*., 2003: 105 – see also Section 4.3.2), scientific kinds are defined *only* by the properties included in a property set *F* and the mechanisms that underlie this property clustering, excluding the particular historical origins of the properties in *F*. This means that in Boyd's account in principle *any* entity that exhibits all or most of the properties in the property set *F* that defines a particular scientific kind, due to this entities' being subject to the causal mechanisms that underlie this particular scientific kind counts as a member of this kind, regardless of whether it has any historical connections to other members of the kind. Scientific kinds in Boyd's account thus are intrinsically spatiotemporally unlimited and do not rest on historical relations among their members, as Boyd (1999b: 79-80) for that matter explicitly asserts. Historical kinds, in contrast, are *always* defined by historical relations that hold among their member entities, such as ancestor-descendant relations or relations of common descent, and hence are intrinsically spatiotemporally restricted. For instance,

[23] Millikan (1999a: 54) claims that "Boyd's homeostatic property cluster kinds are not eternal kinds after all, but historical." In his reply Boyd agrees that historical kinds are accounted for by his theory, but comments that his theory *also* applies to non-historical kinds (Boyd, 1999b: 68, 82-84).

in the case of a particular historical kind *H*, even if an entity would exhibit many of the properties in the property set associated with *H* due to a copying mechanism by means of which *H*'s member entities all have come to show similar properties, the entity still would not count as a member of *H* if its properties have resulted through copying from initial material that is different from the initial material from which the members of *H* have been copied. (Cf. Millikan's (1999a: 56; 2000: 21-22) discussion of artificial historical kinds, all members of which must have been built on the basis of the same plan *token*.) Historical kinds thus are fundamentally incompatible with Boyd's view of scientific kinds.

While Boyd's view provides an adequate account of the explanatory and predictive value of intrinsically spatiotemporally unlimited causal kinds, it does not do so for intrinsically spatiotemporally limited historical kinds. This shows that the view that causal and historical kinds can both be accounted for by a mechanistic (in this case Boyd's) account of scientific kinds is confused.

A second case of conflation of causal and historical kinds is found in recent work by Waters (1998). According to Waters, biologists employ two types of explanatory and predictive empirical generalizations, which he calls 'causal regularities' (i.e., causal generalizations in our terminology) and 'distributions' (i.e., historical generalizations). According to Waters, causal generalizations in biology explain and predict the viability of organisms that exhibit a particular combination of properties (they are design explanations *sensu* Wouters, 1999; 2005); causal generalizations in biology possess a spatiotemporally unlimited domain of validity and exhibit the most important features that are traditionally understood to characterize laws of nature (Waters, 1998: 6, 22). Historical generalizations in biology "(…) simply generalize about current evolutionary fashions." (Waters, 1998: 16). Waters (1998: 16) argues that historical generalizations in biology are accidental generalizations and hence by themselves are not explanatory. What renders historical generalizations scientifically relevant, in Waters' view, is their use to systematize the application of causal generalizations. That is, historical generalizations explain why particular causal generalizations explain particular actual cases (Waters, 1998: 8).[24] Consequently, in Waters' view causal and historical generalizations in biology hold over the same kinds

[24] In this respect Waters' position resembles the position defended recently by Rosenberg (2001; cf. 1985). According to Rosenberg (2001: 755), the historical generalizations of biology are not explanatory by themselves, but constitute explanation sketches that explain by invoking the laws of natural selection.

(Waters, 1998: 13): for a biological kind to be of scientific importance, not only must the associated combination of properties be viable (explained by causal generalizations), evolution must also in fact have produced organisms that exhibit this particular combination of properties (explained by historical generalizations). All biologically important kinds thus in Waters' view are founded on conjunctions of causal and historical generalizations.

As we have argued in Section 4.4.1, generalizations regarding organismal similarities that hold over spatiotemporally limited historical kinds possess explanatory and predictive force in their own right next to generalizations over spatiotemporally unlimited causal kinds. Thus, in Waters' account spatiotemporally unlimited and limited kinds are incorrectly conflated. This can also be seen from the fact that, as Waters (1998: 20-30) acknowledges, causal generalizations in biological science are not bounded by the limits of the taxonomic groups that are formally identified and named by phylogenetic systematics (which are historical kinds). Historical generalizations, however are. The example regarding the similarities in body shape of cetaceans and fish constitutes a case in point: while the causal generalization regarding fusiform body shapes ranges over the non-historical kind 'aquatic organisms', the historical generalization regarding the possession of backbones holds over the historical kind Vertebrata.

4.5. Conclusion

The position that we argued for in this chapter is summarized as follows:

(1) A distinction exists between two types of explanatory and predictive generalizations: law-generalizations and kind-generalizations.
(2) Similarities in the properties of material entities are not explained and predicted by means of law-generalizations but by means of kind-generalizations.
(3) Kind-generalizations can be made over two types of scientific kinds that are based on two different types of underlying factors: causal kinds based on causal mechanisms and historical kinds based on shared history.
(4) Causal kinds are spatiotemporally unlimited, whereas historical kinds are spatiotemporally limited; kinds of both types may however be exceptionless or non-exceptionless.

(5) The criterion of universality that is commonly used to assess the scientific validity of explanations is appropriate for explanations in terms of law-generalizations but misplaced for explanations in terms of kind-generalizations.

Our larger project, however, is not only to defend a theoretical position, but to solve live issues in the philosophy of biology and biological science itself. One important such issue is whether biological taxa, and particularly species, constitute 'good' scientific kinds over which explanatory and predictive empirical generalizations hold.

In this context it is important to note that the interpretation given in Section 4.3.1 of the essentialism of the Kripke/Putnam theory of natural kinds, as hinging on causal mechanisms rather than microcomposition, possesses direct consequences for the long-standing issue whether species in biology can be conceptualized as (natural) kinds. Because both Kripke and Putnam repeatedly suggested that the essences of biological kinds of organisms were probably to be sought in genetic structure (e.g., Putnam, [1970] 1977: 104; 1983: 73), a common objection to suggestions that species are natural kinds consists in the argument that intra-species genetic variability and inter-species genetic similarity are too large to allow for any genetic species essences to be possible. Placing primacy on the shared causal mechanisms that lead from genotype to phenotype rather than on a purportedly shared genotype defuses this argument against the Kripke/Putnam theory, because genetic (microcompositional) similarity is no longer a strict requirement for kind membership.

Now that the theoretical groundwork is (largely) done, the question whether explanatory and predictive generalizations hold over species and higher biological taxa, that is, whether species and higher taxa can be conceptualized as causal kinds (as Boyd, 1999a, and Griffiths, 1997; 1999 suggested) or historical kinds (as has been suggested by Millikan, 1999a; 2000), can be addressed elsewhere (Chapter 5).

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5 Generalizations and kinds in natural science: The case of species

Abstract

Traditionally, species in biological science are perceived as scientific kinds of organisms over which explanatory and predictive generalizations can be made. This view seems in conflict with the nowadays widely accepted ontological position that species are not kinds or classes at all, but individuals. The present chapter addresses the question whether on the ontology of species as segments of the tree of life, species can be conceptualized as scientific kinds. Criticizing the positions advanced recently by Paul Griffiths and Ruth Millikan, it is argued that on this ontology of species, a conceptualization of species as natural kinds is not possible and that a conceptualization as historical kinds is possible only on the adoption of a particular definition of species as tree-segments: the *Composite Species Concept* as introduced by Kornet & McAllister.

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"Inductions from one member of a species to the next often hold up for very good reason. Were this not so, there could be no science of biology." (Millikan, 2000: 208)

5.1. Introduction

A crucial aspect of scientific investigation is the identification of kinds of entities over which explanatory and predictive generalizations hold. Traditionally, the species of organisms that stand at the focus of biological investigation have been counted among the prototypical examples of such scientific kinds. However, following the demise of essentialism in systematic biology in the 1960s and some subsequent debate in the 1970s-1980s on the issue whether species could be conceptualized as natural kinds, at present the generally accepted view is that species are themselves entities (individuals) that constitute subjects of biological case studies, rather than kinds of entities over which scientifically important generalizations hold (for an overview of the arguments, see Rosenberg, 1985: 201-212).

This change in the ontological status of species notwithstanding, a central part of biological science still consists in the making of generalizations that are supposed to hold over all and only the member organisms of one species, based on the study of just a few of its member organisms. To give an example from empirical investigation:

> "Three giant clams (*Tridacna maxima*) were collected (…). The clams did not react to static stimuli, but responded very strongly to gratings whose phase changed suddenly (…). This response was used to determine the eyes' spatial resolution (…). I have shown that the pinhole eyes of giant clams produce images that can resolve stripe patterns with periods between 13.9° and 20.7°." (Land, 2003).

In statements like this, species are – to the disregard of their precise ontological status – in fact conceptualized as scientific kinds of organisms over which explanatory and predictive generalizations hold. Thus, the empirical results found by Land (2003) allow to explain the optical resolution of the eyes of a given organism as a property that any organism would very probably exhibit, if it belonged to the species *T. maxima.* Similarly, they allow to reliably (be it not unfailingly, depending on the natural factor

underlying the generalization at stake) predict that future organisms of the species *T. maxima* will possess pinhole eyes with a resolving capacity between 13.9° and 20.7°.

The general question with which the present chapter is concerned, is on which basis a conceptualization of species as scientific kinds can rest. More specifically, the issue addressed here is whether the widely accepted ontology of species as segments of the phylogenetic tree of life is compatible with a conceptualization of species as scientific kinds.

Only quite recently has the idea of biological taxa as scientific kinds been revived in the philosophical debate and have new arguments been presented in support of the position that biological taxa, particularly species, can and should be conceptualized as scientific kinds of organisms. Three authors in particular have argued in this direction: Richard Boyd (e.g., 1999a; 1999b; 2000; Keller *et al.,* 2003), Paul Griffiths (1994; 1996a; 1997; 1999) and Ruth Millikan (1998; 1999a; 1999b; 2000).[25] In this chapter I focus on Griffiths' and (to a lesser extent) Millikan's accounts. Both authors have defended the position that on adoption of the ontology of species as segments of the phylogenetic tree of life, species can be conceptualized as scientifically important kinds of organisms. Both, however, have insufficiently specified how the factors that are identified as underlying biological kinds of organisms are able to account for the possibility of making explanatory and predictive generalizations over organisms of the same tree-segment. In addition, neither author takes into account the differences between the various sorts of tree-segments[26] that have been advanced in the literature as candidates for species status. The present chapter revolves around these two issues.

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[25] For example: "The species category (…) is supposed to reliably collect morphological, physiological, and behavioral properties. We can investigate these properties in the species as a whole by studying a few members of the species. That being accomplished, we can explain the fact that an individual has certain properties by citing its species: any organism that *was* of this species *would* have these properties." (Griffiths, 1999: 215; original italics); and: "[I]n the case of many sciences, observations need to be made of only one or a very few exemplars of each kind studied in order to determine that certain properties are characteristic of the kind generally. If I have determined the boiling point of diethyl ether on one pure sample, then I have determined the boiling point of diethyl ether. (…) Similarly for determining the placement of the kidneys or the number of chromosomes in *Rana pipiens*." (Millikan, 1999a: 48-49).

[26] In the present chapter, I use 'tree-segment' as a generic term to denote segments of the tree of life, defined by the historical (ancestor-descendant) relations that exist between

In sum, I shall argue for the following two main claims:

I. The factors that are responsible for the persistence of organismal traits over multiple generations by themselves are not sufficient to underlie phylogenetic tree-segments as scientific kinds of organisms over which explanatory and predictive generalizations hold.

II. In order to be conceptualizable as scientific kinds, tree-segments need to be defined by apomorphic character states. However, phylogenetic taxa defined by apomorphies cannot without further qualification be conceptualized as scientific kinds. More specifically:

(1) Segments of the tree of life on any taxonomic level intrinsically cannot be conceptualized as *causal kinds* of organisms, supported by causal mechanisms.

(2) *A fortiori*, segments of the tree of life on the taxonomic species level cannot be conceptualized as *natural kinds* (contra Griffiths, 1997; 1999).

(3) Of the three most important sorts of tree-segments that have been advanced as candidates for species status – *internodons*, *clades* and *branches* – only branches and those clades that are defined by apomorphies can be conceptualized as *historical* kinds over which generalizations hold that can feature in scientific explanation and prediction.

(4) Clades can be conceptualized as historical kinds, but cannot be attributed species status. Therefore, in order to conceptualize species-level tree-segments as historical kinds these have to be understood as branches on the tree of life (i.e., as composite species *sensu* Kornet & McAllister, 1993; 2005).

In Section 5.2, the background of the present work is given: the term 'species' possesses multiple meanings, which have to be clearly distinguished when considering

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the organisms that constitute them. As is explicated in Section 5.4.2 and Figure 5.1, various sorts of tree-segments should be distinguished: internodons, clades and branches (I use the terms 'internodon', 'clade' and 'branch' as strictly defined technical terms). The differences between these sorts of tree-segments become important in the last part of this chapter. Where 'tree-segment' is used, all of these sorts are meant.

the question whether species can be conceptualized as scientific kinds; in addition, two sorts of scientific kinds must be distinguished: causal kinds (encompassing natural kinds) and historical kinds. In Section 5.3, I substantiate claim I. In Section 5.4, I attempt to establish claim II, arguing that the ontology of species as segments of the tree of life is incompatible with the nature of causal kinds (II.1) and natural kinds (II.2) and investigating how, alternatively, tree-segments could be conceptualized as historical kinds (II.3-II.4).

5.2. Preliminary issues: the different meanings of 'species' and 'kind'

The question whether – and if so, how – species can be conceptualized as kinds of organisms over which explanatory and predictive generalizations reach cannot be answered without prior qualification of the terms 'species' and 'kind'. The term 'species' as it is used in present-day biology possesses multiple different sorts of material referents, which must be clearly distinguished in discussions on the epistemology and ontology of species (cf. Chapter 3). In addition, two sorts of scientific kinds are to be distinguished over which explanatory and predictive generalizations hold: causal kinds and historical kinds (cf. Chapter 4). In this section, I address these issues in turn.

5.2.1. 'Species' denotes four scientific concepts

Most biological and philosophical discussions of the notion of species implicitly presuppose that the term 'species' refers to a single scientific concept. That is, most authors take the view that all species are of the same or at least a very similar sort (either classes of organisms, or diachronic lineages, or synchronic systems of populations, etc.) and that the term 'species' thus refers to a single scientific category, connected to a single scientific concept. The species problem, then, is understood as the quest for the one nature of species and the one correct definition of 'species'.

Although it may seem that this presupposition is typical for monistic accounts of species, this is not the case. Many (be it not all) authors who subscribe to one or other form of species pluralism – i.e., the view that the species category is not a homogeneous category – also take this view. (See Reydon, 2005, for further discussion – here Chapter 3.) Consider for example three prominent versions of species pluralism that have been advocated in the literature: Kitcher's (1984) 'pluralistic realism', Mishler & Brandon's

(1987) version of species pluralism and Ereshefsky's (1992) 'eliminative pluralism'. According to Kitcher, all "[s]pecies are sets of organisms related to one another by complicated, biologically interesting relations" (1984: 309). However, Kitcher argues, there are many such relations that can stand at the focus of biological research, none of which is privileged, and therefore there are many different ways of clustering organisms into sets that are to be attributed species status. Mishler & Brandon, in turn, hold that all species are clades (i.e., monophyletic tree-segments – see Section 5.4.2), but take the view that different criteria for attributing species status to clades are to be used for the study of different organism groups (1987: 406). Ereshefsky, lastly, defends species pluralism while adopting the ontology of species as lineages in the tree of life: while all species are lineages, "[t]he forces of evolution produce at least three different types of basal lineages (…) that cross-classify the organic world. (…) Consequently, the tree of life on this planet is segmented into a plurality of incompatible but equally legitimate taxonomies." (1992: 679).

I have argued elsewhere (Reydon, 2005 – here Chapter 3) that the above presupposition – that the term 'species' possesses a single sort of referent and thus denotes a single scientific concept – is mistaken. An examination of how the term is used in contemporary biology and in the present philosophical debate on the species problem has shown the term to possess four different sorts of referents, all of which constitute units that are subjects of biological investigations. Because of the differences in ontological status of these four sorts of referents, the term 'species' cannot be understood as denoting one single overarching concept of species, but must be understood as denoting four distinct scientific concepts. That is, the term 'species' as it is used today is a homonymic term that functions as the placeholder for four distinct scientific concepts, all of which at present occupy a place in biology's conceptual framework:

- the concept of *evolveron* – evolverons are entities that participate as wholes in evolutionary processes; they are systems of synchronous populations that participate as wholes in evolutionary processes; Mayr's widely adopted *Biological Species Concept* is a definition of 'species' that understands species in this way;
- the concept of *phylon* – phylons are the basic segments of the tree of life; phylons are static parts of the historical pattern of evolution of life on earth, that is, the passive products of evolution (for examples see Section 5.4.2);

- the concept of *organism-kind* – organism-kinds are classes of organisms that exhibit similarities in their structural and/or behavioral properties; in the traditional *Morphological Species Concept* species are thus conceptualized;
- the concept of *evolveron-kind* – evolveron-kinds are classes having evolverons that occupy similar positions in evolutionary dynamics as their members; the notion of *Evolutionary Significant Unit* (discussed in Mayden, 1997) is an example.

In order to clearly distinguish between these four concepts and to detach them from the historically burdened term 'species', I have introduced four proper names to denote the concepts involved (rather than using terms like 'phylospecies', etc.).[27]

Because of this fourfold homonymy of the term 'species', the question whether species can be conceptualized as scientific kinds over which explanatory and predictive generalizations hold – and the accounts offered by Griffiths and Millikan, addressed later in this chapter – cannot be addressed straightforwardly, without establishing the precise meaning in which the term is used. Note that Griffiths and Millikan do not distinguish between the different meanings of 'species'; in their accounts of species as scientific kinds both adopt without much argumentation an ontology of species as phylogenetic tree-segments (i.e., phylons), but endorse different views of which sorts of tree-segments constitute candidate species. (In Section 5.4.2, Griffiths' and Millikan's understanding of species as tree-segments will be considered in more detail.)

5.2.2. There are two sorts of scientific kinds

A second issue that must be addressed prior to turning to the main topic of this chapter, is the distinction between two types of scientific kinds, causal kinds and historical kinds. Following this distinction, the question whether species can be conceptualized as

[27] For arguments and further discussion of this position, I refer to Reydon (2005 – here Chapter 3). It is however important to note that I have not advocated the position that all four concepts *should* be incorporated in the conceptual framework of biological science. Rather, I have presented the diagnosis that at present they *are* incorporated in biology's conceptual framework; whether their placement in the conceptual framework of biology will in the end prove legitimate, is a matter for the future development of biological science to decide.

scientific kinds subdivides into two questions (bracketing the distinction between the four meanings of 'species' discussed above): Can species be conceptualized as causal kinds? and Can species be conceptualized as historical kinds? I address these questions in Section 5.4, taking, as said, 'species' in the meaning of 'tree-segments'.

On the traditional view in philosophy of science, explanatory and predictive generalizations in science are made over the members of natural kinds, that is, kinds of entities that exhibit similar structural and behavioral properties due to their having the same underlying essence. Usually, this view entails an understanding of the essences of natural kinds as consisting in shared microstructural properties, possession of which is necessary and sufficient for kind membership. However, as was already implied in Putnam's (1983) account of natural kinds and was argued in detail elsewhere (Reydon & Kornet, subm. – here Chapter 4), the primary factors that underlie natural kinds and account for the possibility of making explanatory and predictive generalizations over the members of such kinds consist in shared causal mechanisms rather than shared microstructure. That is, the fact that the member entities of a given kind exhibit similar structural and behavioral properties is explained and predicted not so much by referring to shared essential properties but by referring to the causal mechanism(s) to which the member entities of the kind are subject and that account for the potential existence of material entities that possess the properties in question.

Reydon & Kornet (subm. – here Chapter 4) argued that two different sorts of factors may be responsible for similarities in material entities and that consequently two sorts of scientific kinds should be distinguished. The kinds of entities of which the similar properties are due to multiple instances of operation of the same causal mechanism(s) are called *causal kinds* by Reydon & Kornet (subm. – here Chapter 4), who argued that natural kinds as traditionally conceived should be understood as constituting a subcategory of the category of causal kinds. (For natural kinds the defining causal mechanisms account both for the stable persistence of the material entities in question and for some of their properties, while for causal kinds in general these mechanisms account only for some of their properties – for extensive discussion, see Reydon & Kornet, subm. – here Chapter 4.) Because the causal mechanisms that underlie causal kinds will in principle cause multiple independent instantiations of entities at any spatiotemporal location, given that the right conditions obtain, causal kinds are inherently spatiotemporally unlimited. The kinds of entities of which the similarity is due to these entities' shared history are called *historical kinds*. By being founded on a particular historical event in which a particular property originated, historical kinds – in contrast to causal kinds – are intrinsically spatiotemporally limited,

that is, only those entities that stand in the proper historical relation to the historical event underlying a particular historical kind can count as a member of this kind. Scientific generalizations over the members of both causal kinds and historical kinds may be exceptionless, as well as non-exceptionless. (See further Reydon & Kornet, subm. – here Chapter 4.)

It should be remarked here that Millikan makes a distinction between two types of scientific kinds similar to the above distinction.[28] According to Millikan, species and higher taxa, which she conceptualizes as segments of the tree of life, are historical kinds (1999a: 54-55; 1999b: 101; 2000: 23-24, 208). Griffiths' position is less univocal, because Griffiths does not distinguish between the different sorts of scientific kinds. Griffiths' view can be interpreted in two ways. On the one hand, Griffiths asserts to hold a conceptualization of species (that is, species-level clades) as natural kinds with historical essences. On this reading, Griffiths' position is interpreted as a conceptualization of tree-segments as causal kinds that rest on causal mechanisms. (In Section 5.4.1, I argue that this does not constitute a feasible conceptualization – it is therefore very apt that Griffiths (1999) describes his project as an attempt at 'squaring the circle'.) On the other hand, Griffiths asserts that "[n]othing that does not share the historical origin of the kind can be a member of the kind" (1999: 219), thus seemingly advocating a conceptualization of species as historical kinds. I am not concerned here with establishing the correct reading of Griffiths' position, but shall consider both interpretations in Section 5.4.

5.3. Phylogenetic inertia is not enough

The making of explanatory and predictive generalizations over a group of organisms with respect to the possession of a particular trait is possible only if factors are identified that underlie the persistence of the trait in question over a period of time throughout this group of organisms. From the perspective of contemporary biology trait persistence may be due to two distinct sorts of underlying factors, one of which can underlie both causal kinds and historical kinds of organisms, while the other can only underlie historical kinds of organisms. Below I outline the nature of these factors (Section 5.3.1) and show

[28] Millikan's account of the two types of scientific kinds however differs on various points from the account given here. See Reydon & Kornet (subm. – here Chapter 4) for discussion.

that by themselves they are insufficient to underlie tree-segments as scientific kinds on the level of species, because the time periods over which they occur do not coincide with the temporal extent of species-level taxa in the tree of life (Section 5.3.2). What is needed in addition, I shall argue in Section 5.4, is a particular character state that has originated for the first time in this particular segment of the tree of life – that is, an apomorphy (see Hennig, 1965: 105; 1966: 89) – that in combination with one or more of these factors can define tree-segments as kinds of organisms.

5.3.1. Two sorts of factors that underlie kinds of organisms

In present-day biology two distinct sorts of factors are recognized that can account for the persistence of a particular organismal trait over longer periods of time. The distinction between these two sorts of factors traces back to Darwin, who asserted that organisms are "formed on two great laws": unity of type and the conditions of existence (1859: 206). Griffiths (1996a; 1996b; 1999) provided an explication of these two sorts of factors in terms of the notion of *phylogenetic inertia*. In the discussion below, I follow Griffiths' terminology in order to connect the discussion directly to both Griffiths' explication and the discussion in the biological literature regarding the phenomenon of phylogenetic inertia.[29]

According to Griffiths, the phenomenon that allows for explanatory and predictive generalizations to be made over the members of the same segment of the tree of life is phylogenetic inertia:

> "[P]hylogenetic inertia is what licenses induction and explanation of a wide range of properties – morphological, physiological, and behavioral – using kinds defined *purely* by common ancestry. If we observe a property in an organism, we are more likely to see it again in related organisms than in unrelated organisms." (Griffiths, 1999: 220; emphasis added).

I shall first consider Griffiths' claim that phylogenetic inertia is *the* factor that underlies scientific kinds of organisms, a claim that by itself leaves room for conceptualizations of

[29] For biological discussions of the notion of phylogenetic inertia, see Wilson (1975: 32-37), Edwards & Naeem (1993: 773), Reeve & Sherman (1993: 18-19) and Blomberg & Garland (2002).

species as scientific kinds of either type. I shall return to Griffiths' idea of kinds defined *purely* by common ancestry in Section 5.4.3.

Although in contemporary biology the notion of phylogenetic inertia is widely used in empirical studies as the *explanans* that explains the persistence of organismal properties and similarities between organisms of different groups (Blomberg & Garland, 2002: 901-902), it is not a well-defined notion and various meanings of the term are used simultaneously. While some authors use the term to denote the *phenomenon* that particular organismal traits are retained throughout large parts of the phylogenetic tree of life notwithstanding changes in the environment in which subsequent generations of organisms live (e.g., Edwards & Naeem, 1993: 773; Reeve & Sherman, 1993: 18-19), others use the term to denote the *underlying factors* of this phenomenon such as environmental factors or the intrinsic properties of evolving populations (e.g., Wilson, 1975: 32-37; see also Blomberg & Garland, 2002: 900). The former meaning is the most common and this is the meaning in which Griffiths uses the term (although Griffiths does not spell this out). Phylogenetic inertia in this meaning is thus itself a phenomenon in need of an explanation, rather than a factor that can be invoked without further elucidation to explain and predict similarities of the organisms in a particular tree-segment.[30] Griffiths provides the following elucidation.

Griffiths (1996a: S1-S2; 1996b: 524-528, 1999: 220) makes a distinction between two types of phylogenetic inertia, each due to a different sort of cause. Using an analogy to the concept of inertia in physics, Griffiths calls these 'Aristotelian phylogenetic inertia' (henceforth API) and 'Newtonian phylogenetic inertia' (NPI).[31]

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[30] It is noteworthy that biologists do not commonly apply the notion of phylogenetic inertia to similarities between organisms within a single species. Phylogenetic inertia is usually understood as consisting in the occurrence of similarities between organisms belonging to different species or higher taxa (cf. Blomberg & Garland, 2002; an exception is Wilson (1975: 37), who holds the view that phylogenetic inertia can also occur on and below the species level). This conflicts with Griffiths' understanding of phylogenetic inertia as occurring within a single species as well as between different species and higher taxa.

[31] The distinction between two types of phylogenetic inertia is also found elsewhere, be it less explicitly (e.g., Reeve & Sherman, 1993: 18-19; Blomberg & Garland, 2002: 902). Millikan makes a similar distinction in her assertion that the organisms in a particular segment of the tree of life will tend to resemble each other because of the fact "(…) (1) that something akin to reproduction or copying has produced all the various kind

Aristotelian Phylogenetic Inertia. In an instance of API, the underlying factor is stabilizing selection. After having become fixated in an ancestral population, a particular organismal trait remains present in descendant organisms due to stabilizing selective factors that actively maintain the persistence of adaptive traits throughout the tree-segments in which they first arose. When the selective force is removed, the corresponding trait tends to gradually disappear. In cases of API, the invoked selective factors explain both the *origin* of a trait (that is, its first fixation in a population after it has originated through spontaneous mutation) and its *maintenance* throughout the tree-segment in which it originated (Reeve & Sherman, 1993: 18; Griffiths, 1996b: 524-528; 1999: 220; Blomberg & Garland, 2002: 902). The selective factors that underlie instances of API pertain to the population level or higher organizational levels (contrary to Griffiths' suggestion[32]).

As a type of *phylogenetic* inertia, API is a phenomenon that intrinsically involves phylogenetic tree-segments. The occurrence of API thus may in some cases account for historical kinds of organisms over which explanatory and predictive generalizations hold, that is, single continuous tree-segments consisting of organisms that are united by common history.

Because the factors underlying stabilizing selection operate on units of evolution independently of their history, in some cases they will underlie causal – rather than historical – kinds of organisms, that is, kinds that include organisms from multiple separate tree-segments. (Recall that Griffiths does not distinguish between these two

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members from one another or from the same models (e.g. from genes replicated from the same gene pool) and (2) that the various kind members have been produced in or in response to the very same ongoing historical environment" (1999a: 55; cf. 1998: 58; 2000: 19-20, 208). Although Millikan's account is not framed in terms of the notion of phylogenetic inertia, it is translatable into such terms without much difficulty.

[32] Griffiths sketches the following scenario for API: "Like a body in Aristotle's theory of motion, an organism subject to selective forces gains a certain quantity of 'inertia'. When the selective force is removed this inertia maintains the organism in its current, adapted state. The inertia eventually runs down, and the organism reverts to an undifferentiated state." (1996b: 524). This way of understanding API, however, is not correct, for it is not individual *organisms* that acquire 'inertia' and eventually return to an undifferentiated state after removal of selective environmental factors, but evolving groups of organisms (that is, evolverons).

sorts of scientific kinds.) Similar environments will exert similar selection pressures on any evolving unit that is present in them. The consequence is convergent or parallel evolution: organisms in different independently evolving units (evolverons) that are immersed in the same environment will be likely to eventually exhibit the same adaptive properties, provided that they have the appropriate resources at their disposal. (Note that these resources need not necessarily be the same, nor do they have to related by common descent.) In principle all organisms that exhibit a particular trait due to the working of the same selective factors on similar evolving units can thus – irrespectively of the presence or absence of historical connections between them – be counted as members of the same kind, i.e., the causal kind of which these selective forces constitute the underlying factor.

An example of convergent evolution resulting in causal kinds of organisms concerns the streamlined fusiform body shape of cetaceans and many fish: both cetaceans and many fish possess streamlined torpedo-shaped bodies as an adaptation to their life in open water. This similarity cannot be explained by historical factors, since the same body shape occurs in two separate tree-segments that do not share their most recent ancestor and different developmental pathways are responsible for body shape in the two organism groups. (If the same developmental pathway were responsible for this similarity in body shape, the similarity could be attributed to the occurrence of NPI – see below.) The generalization that explains the occurrence of torpedo-shaped bodies thus ranges over a causal – rather than historical – kind of organisms (see Reydon & Kornet, subm., for extensive discussion of this example – here Chapter 4).[33]

Newtonian Phylogenetic Inertia. In contrast to API, NPI occurs in the absence of relevant selective factors, when traits that have come into being in the past remain present in a tree-segment until environmental changes result in a selective factor that actively causes their disappearance. Instances of NPI can be explained in terms of the presence of factors that operate on or below the organism level, such as developmental mechanisms and constraints, the origins of which are accounted for historically:

[33] This does not imply that the causal kind in question is the only kind to which these organisms can be counted, nor that this kind is important in all research contexts. While the explanation of the similarity in body shape of cetaceans and many fish requires a generalization that reaches over a particular causal kind, with regard to other properties the same organisms will probably need to be attributed to different causal or historical kinds.

instances of NPI reflect the fact that "(…) all organisms carry evolutionary "baggage."" (Reeve & Sherman, 1993: 19; cf. Edwards & Naeem, 1993: 773; Blomberg & Garland, 2002: 901). Such developmental factors may consist, for instance, in close linkage of a trait to other traits in the developing organism (Griffiths, 1996a: S6-S7; 1996b: 525-526; 1999: 220-221) or a low degree of variability in the genetic basis on which descendant organisms can develop (Wilson, 1975: 33-34; Reeve & Sherman, 1993: 18-19). These factors can explain the presence of a particular trait in a particular group of organisms, as well as its absence in some organisms that belong to this group (the latter for example by pointing to a failed linkage to other traits in the organisms' development or the occurrence of a deleterious mutation – see also note 35 on p. 123). Because the factors that are invoked to explain instances of NPI are inherently rooted in the history of the evolutionary unit to which the organisms under consideration belong, these factors can only underlie historical kinds of organisms.

Summarizing, two sorts of factors may be responsible for the maintenance of a trait throughout a group of organisms: external selective factors that may underlie both causal and historical kinds of organisms (the latter in instances of API that occur within a single segment of the tree of life) and internal organismal factors that can underlie only historical kinds of organisms (in instances of NPI). Both types of phylogenetic inertia are found in nature. Conservation of traits such as color and the presence of eyesight are instances of API, conservation of the pentadactyl limb in tetrapods exemplifies NPI (these are examples provided by Griffiths, which I consider in the next subsections). Note that in principle the persistence of a particular trait throughout one segment of the tree of life does not necessarily constitute an exclusive instantiation of either NPI or API; a particular instance of trait conservation may also be due to a combination of both phenomena.

5.3.2. Why phylogenetic inertia alone cannot support scientific kinds of organisms

According to Griffiths (1999: 220; quoted above), phylogenetic inertia is what grounds explanatory and predictive generalizations regarding organismal properties. However, the occurrence of phylogenetic inertia by itself is insufficient to underlie generalizations over the member organisms of those segments of the tree of life that biologists recognize and formally name as species. That is, although the occurrence of phylogenetic inertia may indeed be a necessary requirement for the possibility of making such generalizations, it is not a sufficient requirement.

The reason is that the time periods over which instances of phylogenetic inertia occur do not normally coincide with the temporal extents of basic tree-segments. Instances of NPI tend to persist over much longer periods of time than the temporal extent of species-level tree-segments, thus allowing for generalizations of which the domain of validity extends far beyond the boundaries of the tree-segments that are identified as species. In contrast, instances of API tend to persist only over periods that are much shorter than the temporal extent of species-level tree-segments. Because the parts of the tree of life in which API occurs in most cases are not separated from the rest of the tree by permanent splits, these parts are not recognized as independent biological taxa.

Consider an instance of NPI, discussed by Griffiths: conservation of the pentadactyl limb throughout the monophyletic tree-segment (superclass) Tetrapoda, a textbook example of a homologous organismal trait (see, e.g., Ridley, 1996: 53-54). Griffiths (1996a: S6-S7; 1999: 220-221) points out that the high degree of conservation of traits like this is explained by their being deeply rooted within the developmental pathway of the organisms in question. As a consequence of this deep developmental entrenchment, however, the presence of pentadactyl limbs is not limited to a single monophyletic tree-segment on the taxonomic level of species. Galis *et al.* (2001) recently considered the evidence for the hypothesis that changes in the number of digits in tetrapods are associated with negative pleiotropic effects that reduce the chance for the organism's survival, rendering tetrapod pentadactyly a highly conserved trait because of its firm embedding in organismal development. In three of the tetrapod classes, Reptilia, Aves and Mammalia, limb development is strongly integrated into the development of the embryo as a whole. Changes in limb development thus may cause a large number of negative pleiotropic effects in the entire organism. In the fourth tetrapod class, Amphibia, limb development is much less interconnected with the development of the rest of the embryo and the negative pleiotropic effects of changes in limb development are largely limited to the limbs themselves. These effects are however still sufficient to cause conservation of pentadactyly in the class Amphibia. Instances of extreme NPI like tetrapod pentadactyly thus usually ground generalizations over tree-segments on taxonomic levels far above the species level.

Note that the fact that a particular trait is deeply rooted in a conserved developmental pathway does not necessarily imply that this trait is actually present in *all* organisms that possess this pathway. Recent work on wing evolution in stick insects, for example, has suggested that although the genetic developmental pathway for wing formation has been conserved throughout the entire monophyletic tree-segment of

'winged' insects (the subclass Pterygota), evolutionary loss of wings may occur by means of silencing of this pathway followed by subsequent re-evolution of wings through re-expression of the developmental pathway for wing formation (Whiting *et al.*, 2003). Similarly, pentadactyl limbs are not present throughout the entire clade Tetrapoda (Fong *et al.*, 1995: 251-252). While the developmental pathway for the traits in question is present in all organisms of the clade, the generalizations regarding the presence of the expressed traits thus may exhibit exceptions (but this does not diminish their scientific value; cf. note 35 on p. 123; Reydon & Kornet, subm. – here Chapter 4).

The opposite phenomenon, where generalizations are supported only over much shorter periods in the tree of life than the temporal extent of species-level tree-segments, is exemplified by instances of gradual loss of phylogenetic inertia with the disappearance of the external stabilizing selective factor (API), such as loss of color and eyesight in cave-dwelling animals. This can occur without any associated splitting event – that is, without the origin of a new species-level tree-segment – in cases where the entire extant population in a particular tree-segment becomes immersed in a new environment in which color and eyesight no longer constitute selective advantages. In such cases phylogenetic inertia regarding these characters occurs only over the earlier part of the tree-segment and generalizations ranging over the species-level tree-segment's entire evolutionary lifetime are not supported.

In addition, cases in which only part of the extant part of a species-level tree-segment experiences evolutionary loss of particular traits due to invasion of a new environment are not generally recognized as speciation events in actual biological research. In such cases, the occurrence of API regarding the trait in question is limited to a minor part of the tree-segment, that is not separated from the tree-segment by a permanent split and consequently is not recognized as independent taxon.

Consider for instance the amphipod species *Gammarus minus* and the fish species *Astyanax mexicanus*. Both *G. minus* and *A. mexicanus* encompass populations that live in caves as well as populations that live on the surface. In both species the cave populations are thought to have originated in multiple independent invasions of caves by surface populations that, after having invaded the cave, have gradually lost eyesight and pigmentation (these traits having been retained in the surface populations) because of the replacement of the selective conditions in which eyesight and pigmentation constituted an adaptive advantage with different selective conditions. Notwithstanding the divergent evolution of the cave-dwelling and the non cave-dwelling populations, all are counted as belonging to the same species (for *G. minus*: Jones *et al.*, 1992; Fong *et al.*, 1995; Jeffery, 2001: 2; for *A. mexicanus*: Jeffery, 2001; Porter & Crandall, 2003: 544; Tian &

Price, 2005). In the cases of *G. minus* and *A. mexicanus* the phylogenetic inertia (API) of eyesight and pigmentation continues to occur in non cave-dwelling populations due to the presence of stabilizing selective forces but has gradually faded away in cave-dwelling populations of the same species that live synchronously. While the occurrence of phylogenetic inertia with respect to traits like eyesight and pigmentation does ground generalizations that explain the properties of some organisms that belong to *G. minus* and *A. mexicanus*, these generalizations pertain only to a limited part of the organisms belonging to these species.

Other examples show that this problem is not limited to one single trait of the organisms in question, while they share all or most other traits. Guppies (*Poecilia reticulata*), for instance, occur on Trinidad in isolated populations that "differ in virtually every feature that biologists have cared to examine" (Magurran, 1998: 276). Morphological and behavioral traits of the organisms belonging to *P. reticulata* are highly dependent on environmental circumstances (particularly predator presence) and are found to change rapidly when a population is transplanted to a different environment. Yet, all populations are counted as belonging to the same species because of the lack of reproductive isolation between them: gene flow remains present between populations that live largely separated and of which the member organisms exhibit different traits, thus preventing the separations between populations from becoming permanent (Magurran, 1998).

It should be noted that API does not only result in generalizations that hold over comparatively short periods *within* a single species-level tree-segment. Since splitting events do not necessarily coincide with evolutionary changes in organismal traits, instances of API may occur that transgress the boundaries between two species-level tree-segments. In such cases the situation occurs that inferences from an organism in the ancestral tree-segment just before the splitting event to an organism in a descendant tree-segment just after the splitting event hold up with better reliability than inferences from one organism to another organism that is present at a later time within the same tree-segment.

The above discussion has shown that an account of species-level tree-segments as scientific kinds cannot be achieved in terms of phylogenetic inertia alone: while NPI and API both occur in nature, there is no guarantee that the period of occurrence of an instance of phylogenetic inertia will be wholly or largely coextensive with the temporal extent of any species-level tree-segment. If it is indeed the case that NPI constitutes an implausibly strong conception of phylogenetic inertia and many conserved traits in fact exhibit some form of API (as suggested by Griffiths, 1996a: S2; 1996b: 525-527; but see

1999: 220), the difficulties regarding API may well constitute a widespread problem regarding generalizations not only over species-level tree-segments but especially over higher-level tree-segments. (According to Griffiths (1994: 207-211; 1997: 189, 208-213; 1999: 219ff. – Section 5.4.2), not only species-level taxa but also taxa on higher taxonomic levels can serve to support scientific generalizations.) The occurrence of phylogenetic inertia in a segment of the tree of life thus by itself does not constitute a sufficient condition by which tree-segments can be defined as scientific kinds of organisms.

I now turn to the question which additional requirements must be met for a conceptualization of tree-segments as scientific kinds to be possible.

5.4. How some sorts of tree-segments can be conceptualized as scientific kinds

Under what conditions can phylogenetic tree-segments be conceptualized as scientific kinds of organisms? As discussed in Section 5.2.2, two sorts of scientific kinds are to be distinguished: causal kinds and historical kinds. In Section 5.4.1, I first argue that the ontology of tree-segments is intrinsically incompatible to the nature of causal kinds. In Sections 5.4.2 and 5.4.3, I investigate which additional requirements tree-segments must meet in order to be susceptible to a conceptualization as historical kinds. In the literature on phylogenetic systematics various sorts of tree-segments have been proposed as candidates for being attributed species status – the three most important ones are discussed in Section 5.4.2. I shall argue that only tree-segments that are defined by apomorphic character states (in addition to the occurrence of an instance of phylogenetic inertia) may be conceptualized as historical kinds of organisms and that, moreover, on the species level only one sort of tree-segment may be thus conceptualized.

5.4.1. Why tree-segments cannot be conceptualized as causal kinds

According to Griffiths, segments of the tree of life on all levels of the biological taxonomic hierarchy

> "(…) are ideal candidates for the real natural kinds in biology. In one important respect they might have been invented as a philosopher's example to support the causal theory of natural kind terms. The true phylogeny

> represents a set of real distinctions in the biological world (…). The exact boundaries and the real basis of these divisions is revealed by evolutionary theory and modern systematics (…)" (1994: 210; cf. 1997: 211).

This position is however problematic: the nature of segments of the tree of life on any level of the taxonomic hierarchy inherently conflicts with a conceptualization as natural kinds as they are usually understood.

The all-important reason is the limited spatiotemporal extent of tree-segments. Tree-segments are essentially defined by the ancestor-descendant relations that exist between their member organisms: a necessary requirement that any organism (except the very first organisms of a novel tree-segment) must meet in order to be a member of any given tree-segment is that it should be descended from other organisms that are members of the tree-segment in question. For the members of causal kinds there is no such requirement. While the member organisms of any segment of the tree of life (up to and including the entire tree) can only be present within a particular limited spatiotemporal region of the universe (only in a particular geographic region and only at times between the origin and extinction of the tree-segment in question), causal kinds are intrinsically spatiotemporally unlimited in that their members may exist at any place or time in the universe where the appropriate conditions obtain. A conceptualization of phylogenetic tree-segments as causal kinds – and thus *a fortiori* as natural kinds (that constitute a subcategory of causal kinds; see Section 5.2.2 and Reydon & Kornet, subm. – here Chapter 4) – of organisms can thus immediately be ruled out. Thus, no additional requirements can be found under which tree-segments can be conceptualized as causal kinds.

Can tree-segments alternatively be conceptualized as historical kinds? Because the answer depends on the precise definition of tree-segments that is adopted, first the different types of tree-segments that have been proposed as candidate biological taxa will be considered before turning to addressing the question in Section 5.4.3.

5.4.2. Three sorts of phylogenetic tree-segments

Both Millikan (1998; 1999a; 2000) and Griffiths (1994; 1996a; 1997; 1999 – at least on one reading of his position; see Section 5.2.2) have proposed that species-level tree-segments can be conceptualized as historical kinds of organisms over which explanatory and predictive generalizations hold. However, both authors hold a different understanding of which sorts of tree-segments should be attributed species status. This

difference is important because, as I shall argue below, not all sorts of tree-segments are susceptible to a conceptualization as historical kinds on the taxonomic level of species.

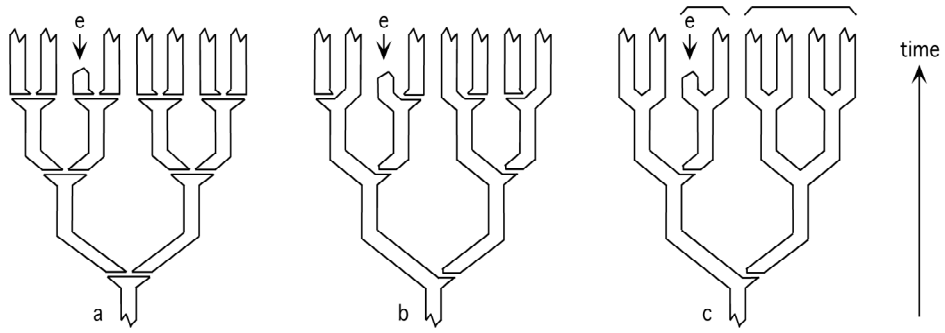

Figure 5.1. Schematic representation of a phylogenetic tree divided into (a) internodons, (b) branches and (c) clades. Note in (c) that the complement of any monophyletic tree-segment (clade) is inherently paraphyletic, implying that phylogenetic trees cannot be exhaustively divided into non-overlapping clades. ('e' denotes a dead end in the tree.)

In the literature various sorts of phylogenetic tree-segments have been advanced as candidates for holding species status, the most important of which are: *internodons*, *branches* and *clades* (see Figure 5.1).

In the classic account of species as tree-segments due to Hennig (1965; 1966), species are defined as those segments of the tree of life between two splitting events or between one splitting and one extinction event (Figure 5.1a; Hennig, 1966: 30-31, 59, 64). This conceptualization of species has later also been defended by Ridley (1989)[34] and is taught in contemporary textbooks on phylogenetic systematics – an example is Wiesemüller *et al*. (2003: 39). On this understanding of species as tree-segments, at any permanent split in the tree of life the ancestral species becomes extinct and two novel descendant species come into being. The segments of the tree of life that are thus defined are the parts of the tree in between its nodes and consequently may be called

[34] Kornet & McAllister (1993: 62-63) pointed out that according to Ridley both temporary and permanent splits should be counted as speciation events, while for Hennig only permanent splits in the tree of life count as such.

'internodons' to distinguish them from other sorts of tree-segments (following Kornet & McAllister, 1993; 2005; cf. Nixon & Wheeler, 1990: 213; Kornet, 1993: 408-409).

Kornet & McAllister (1993: 64; 2005: 99-101) have given two arguments why internodons constitute poor candidates for being attributed species status. Firstly, the allocation of organisms to internodons is dependent solely on the organisms' positions in the genealogical network. Taxonomy, however, is concerned with allocating organisms to species on the basis of organismal character states rather than position in the genealogical network. Secondly and more importantly, internodons generally possess a temporal extent that is too small for them to count as species. To resolve these issues, Kornet & McAllister have introduced the *Composite Species Concept*, according to which species-level tree-segments are clusters of subsequent internodons, consisting of an originator internodon and all of its descendant internodons excluding further originator internodons and their descendant internodons (Kornet & McAllister, 1993: 78; 2005: 114 – an originator internodon being defined as an internodon in which the fixation of a novel character state occurs). Composite species thus are segments of the tree of life that originate in a permanent split in the tree and end in an extinction event (here I call such tree-segments branches – see Figure 5.1b). In terms of internodons, permanent splits in the tree of life are interpreted as nodes in which an ancestral internodon becomes extinct and to two (or more) descendant internodons come into being. In terms of branches, however, permanent splits in the tree are interpreted as nodes in which a new branch branches off from an ancestral one, leaving the ancestral branch in existence (Kornet & McAllister, 1993: 87; 2005: 122-123).

On a third view, species are understood to be the basic monophyletic segments of phylogenetic trees, that is, clades (Figure 5.1c). Under the traditional, cladistic meaning of 'monophyly', monophyletic tree-segments contain *all and only* the organisms that have descended from a particular ancestral population of organisms (Hennig, 1965: 103; 1966: 72-73; Sober, 1988: 16-21; 1992; Kornet, 1993: 426; Griffiths, 1994: 209; 1997: 210). Although the conceptualization of species-level tree-segments as clades is widely endorsed (e.g., Mishler & Brandon, 1987), it amounts to adopting a dubious notion of monophyly. As argued by for instance Nixon & Wheeler (1990: 214) and Kornet & McAllister (1993: 69-71; 2005: 105), the notion of monophyly cannot in general be applied meaningfully on the level of species (see also Wiesemüller *et al.*, 2003: 47-48). One reason is the conflict that arises on the application of the notion of monophyly to species between the accepted insight that species give rise to descendant species and the requirement that species should be mutually exclusive (every organism can at most belong to one species – see Kornet, 1993: 410-412; Kornet

& McAllister, 1993: 69-71; 2005: 105). As soon as an ancestral species gives rise to one (or several) new species, this ancestral species ceases to be monophyletic in the sense that it no longer comprises *all* the descendants of some ancestral population (of course it still comprises *only* descendants of the ancestral population). If the ancestral species did comprise *all* these descendant organisms, it would include its descendant species. In the traditional sense of 'monophyly', therefore, the notion is applied on taxonomic levels above but not on the species level (cf. Hennig, 1965: 98; 1966: 72-73; Wiley, 1981: 7; Sober, 1988: 21; 1992: 204; Kornet & McAllister, 1993: 69-71; 2005: 105).

In the light of the above discussion Griffiths' conceptualization of species as tree-segments shows itself as problematic. According to Griffiths, species are clades containing "(…) *all and only* the descendants of some ancestral group" (1997: 210, emphasis added) and clades on all taxonomic levels can be conceptualized as scientific kinds (1994: 207-211; 1997: 208-213; 1999: 219ff.). At the same time, however, Griffiths (referring to Ridley, 1989) holds that "(…) a species goes extinct whenever it speciates, giving rise to two new species. Each species thus represents the segment of a lineage between two speciation events (…)" (1997: 208), thus adopting a conceptualization of species as internodons. Again, two readings of Griffiths' position are possible, each however facing difficulties. On a strict reading, Griffiths' position is not internally consistent: a species cannot simultaneously be a clade containing *all* descendants of its ancestral population and give rise to descendant species that are distinct from their ancestor. On a more charitable reading, Griffiths conceptualizes species as internodons and understands the terms 'clade' and 'monophyly' in a broader sense, according to which both tree-segments on the species level (non-monophyletic in the traditional sense) and on higher taxonomic levels (monophyletic in the traditional sense) are subsumed under the notion of clade. Although this usage of 'clade' and 'monophyly' is not entirely uncommon (cf. Sober, 1988: 16; 1992), it is confusing to say the least.

Millikan is less clear about the precise nature of her conceptualization of species. Millikan accepts the view that species are individuals (that is "space-time worms" – Millikan, 1998: 58; 2000: 208) and by doing so, also (implicitly) adopts an ontology of species as phylogenetic tree-segments (1998: 58; 1999a: 55; 2000: 19-20, 24 & 203-208). However, Millikan does not seem to explicitly endorse any particular view regarding which sort of tree-segments should be attributed species status.

5.4.3. Which sorts of tree-segments can be conceptualized as historical kinds?

Whether species-level tree-segments can be conceptualized as historical kinds depends on which interpretation of species as segments of the tree of life is actually adopted. Below I shall argue that internodons inherently cannot be conceptualized as historical kinds, whereas branches and clades, that are defined by apomorphic character states, can. Since however clades in the strict sense cannot be attributed species status (as discussed above), in order to conceptualize species-level tree-segments as historical kinds, these have to be understood as branches on the tree of life (i.e., as composite species *sensu* Kornet & McAllister, 1993; 2005).

As argued in Section 5.3, the factors underlying the persistence of organismal traits by themselves are insufficient to define species-level tree-segments as scientific kinds, because in general there is no guarantee that the periods over which traits are conserved will coincide with the evolutionary lifetime of species-level tree-segments. For those tree-segments that are formally attributed the status of taxon in phylogenetic systematics (i.e., that are defined in terms of apomorphic character states), however, a coincidence between trait-conservation period and tree-segment lifetime is present, as is shown below.

Present-day systematic biology is a historical science that aims to reconstruct evolutionary history and to classify organismal diversity on the basis of this historical reconstruction (e.g., Hennig, 1966: 14-24; Wiley, 1981: 6; Wiley *et al*., 1991: 91). The identification, naming and placement of species and higher taxa in the taxonomic system thus essentially rest on the ability to recognize past events by means of the traces that they have left behind. As Sober (1988: 3-5) pointed out, only those historical events that are connected to the present by way of processes that preserve some information regarding past events and states of affairs can be identified in the present. In the case of past splitting events in which new tree-segments have come into being, there is no guarantee that all or even most such events are connected to the present by way of such information preserving processes. There is thus no a priori reason to assume that splitting events will generally be recoverable: whether a particular event in evolutionary history is recoverable, is an empirical matter (Sober, 1988: 1-5). The tree-segments that are formally attributed species status in phylogenetic systematics thus are essentially dependent on our ability to recognize past splitting events in the present by means of organismal character states.

Precisely this issue of recoverability of evolutionary history implicitly surfaced in Hennig's seminal work (1966). Recall that according to Hennig, speciation events

consist in permanent splits in the tree of life: in every splitting event, the ancestral species becomes extinct and two (or more) novel species come into being. Hennig (1966: 88) assumed that such splitting events are always accompanied by a change in the traits of the organisms involved: according to Hennig, in every splitting event at least one character state of the ancestral species is transformed into a different state in at least one of the two daughter species. However, this is not necessarily the case and the fact of the matter is that many splitting events are not accompanied by character state changes (cf. Kornet & McAllister, 1993: 73-77; 2005: 108-114). Since biological systematics is concerned with the partitioning of organismal diversity into species and higher taxa on the basis of organismal character states, only those splitting events that are in fact accompanied by character state changes are identified as past speciation events. The tree-segments that are identified and formally named as taxa in phylogenetic systematics are thus defined by character states that have newly arisen in their evolutionary past, have become fixated in the ancestral population and have been conserved up to the present, that is, apomorphies (Hennig, 1966: 89; Wiley, 1981: 9-10). The combination of an apomorphic character state that is conserved throughout the tree-segment to the present day (that is, an instance of phylogenetic inertia) and the factor underlying this trait conservation is sufficient to define tree-segments as historical kinds.

Because an apomorphic character state necessarily enters into the definition of tree-segments in phylogenetic systematics, it is insufficient to consider tree-segments that are defined *exclusively* by common ancestry as candidate scientific kinds (contra Griffiths' claim; recall (Section 5.3.1) that according to Griffiths tree-segments as kinds of organisms are defined purely in terms of common ancestry). Because internodons are always defined exclusively by the genealogical relations that obtain between their member organisms and organismal character states are irrelevant for internodon membership (Kornet, 1993; Kornet & McAllister, 1993; 2005), internodons intrinsically cannot be conceptualized as historical kinds of organisms. Branches (composite species *sensu* Kornet & McAllister, 1993; 2005) and clades that are defined by apomorphic character states (in addition to common ancestry) can in principle be conceptualized as historical kinds.[35] However, since the identification of clades on the taxonomic level of

[35] Exceptions in the generalizations that hold over these kinds are allowed to a certain extent. Let p stand for the property of combination of properties that is characteristic for members of the kind K. Then it is unproblematic if some kind members do not exhibit p, as long as most kind members do exhibit p. Conversely, it is unproblematic if some non-members of K also exhibit p, as long as most entities that exhibit p are members of K.

species is incompatible to requirements commonly placed on species, clades do not constitute suitable candidates for historical kinds of organisms on the species level (but they do on higher taxonomic levels). Concluding: in order to construe an account of tree-segments as historical kinds on the taxonomic level of species, these tree-segments have to be branches on the tree of life (i.e., composite species *sensu* Kornet & McAllister, 1993; 2005).

Note that the above considerations imply that instances of API in most cases will not constitute good characters for phylogeny reconstruction, because of their short period of conservation compared to the evolutionary lifetime of branches. That is, a particular character will be more likely to be useful for phylogeny reconstruction if its states are conserved in the tree-segment in which these originated by means of developmental factors (NPI) than if character state conservation is due to stabilizing selection (API).

5.5. Concluding remarks

Traditionally, species have performed various roles in biological science, including those of units of classification and units of generalization. Although biologists have traditionally assumed that these roles coincide, this assumption is not necessarily correct (cf. Mayr, 1982: 148-149; Reydon, 2005 – here Chapter 3). A question is thus whether the conceptualization of species as units of classification, i.e., units that can be used in a general reference system for biology, allows to conceptualize species also as units of generalization, i.e., scientific kinds of organisms over which explanatory and predictive generalizations can be made. In the above discussion, the conditions have been explicated under which this question can be answered positively. Still, it remains an empirical issue whether the units of classification that biologists in fact recognize will also prove suitable to serve as units of generalization.

Contemporary systematic biology guarantees the stability of biological classification by founding it upon unchanging evolutionary history and consequently conceptualizing units of classification as segments of the tree of life. The above discussion has shown that in order to render this conceptualization of species in accordance with a conceptualization of species as scientific kinds, species have to be

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(See Reydon & Kornet, subm. – here Chapter 4, for arguments why generalizations over both causal and historical kinds may exhibit exceptions.)

conceptualized as branches in the tree of life, i.e., composite species *sensu* Kornet & McAllister (1993; 2005). Branches as units of generalization constitute historical kinds, not causal or natural kinds. On adoption of the ontology of species as branches in the tree of life, the roles of units of classification and of units of *historical* generalization coincide.

The issue of whether and how species can be conceptualized as scientific kinds has only been partly addressed in the present chapter, in that one out of four meanings of 'species' has been considered. One issue that is still open, for instance, is the question whether the entities denoted by one of the other meanings of 'species' would be susceptible to a conceptualization as causal or even natural kinds. Richard Boyd, for example, repeatedly suggested (without however adopting any explicit ontology of species) that species should be conceptualized as natural kinds of organisms based on what he calls 'causal homeostatic mechanisms' (1991: 142; 1999a; 1999b: 80-82; 2000: 67-68; Keller *et al*., 2003: 105). Evaluating this suggestion will involve a consideration of the other concepts denoted by the term 'species'.

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A Appendix: Species are individuals – or are they?

Abstract

Recently Coleman & Wiley presented a new defense of the species-are-individuals thesis, based on an analysis of the use of binomial species names by biologists. Here I point out some problems in their defense and I argue that although in some domains of biological science species are best understood as individuals, Coleman & Wiley fail to establish that this is true for the whole of biology.

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A.1. Introduction

Recently Coleman & Wiley (2001) presented a new defense of the species-are-individuals thesis (hereafter SAI-thesis). In the debate over the SAI-thesis the issue is usually construed as a straightforward dilemma: either species have the ontological status of individuals, or of classes, without a third option (e.g., Ruse, 1987). Although both sides in the debate are still represented in the literature, most biologists and philosophers nowadays hold the view that species are individuals with organisms as their parts, rather than classes having organisms as members. Those authors who find convincing arguments on both sides of the dilemma usually subscribe to an ontology of species as individuals and attempt to construct an epistemological account of how such individuals can function as kinds (e.g., Griffiths, 1999; Millikan, 1999). Coleman & Wiley defend the SAI-thesis by attempting to disprove the view that species are classes.

Construing the issue as a yes-or-no dilemma is too simple in two respects. Firstly, there is the assumption (which is by no means self-evident) that the issue has but two horns. Traditionally, species have been understood as all belonging to the same category of things and the species problem has been interpreted as the quest for the one true definition of the associated concept. In the last decades several authors have abandoned this monistic stance in favor of so-called 'species pluralism'. As with most '-isms', 'species pluralism' denotes a heterogeneous collection of positions, which however share the view that there are different sorts of species taxa. This view allows a third option: the SAI-thesis is both true and false, depending on the situation considered. Given that there are species taxa of different sorts, not all of them need to be individuals (or classes for that matter). From this perspective the term 'species' is seen to be a homonym, denoting different kinds of things associated with different concepts in different domains of biological research. If this perspective is correct, it follows that the SAI-thesis should be evaluated independently for each distinct concept; findings for one concept need not automatically apply to the other concepts at stake.

Secondly, choosing one of the horns of the original dilemma does not resolve the problem of the ontological status of species. For if species are indeed always individuals, then what kind of individuals are they and are they always of the same kind? There are several feasible options, e.g. interactors (dynamic processes entities) and lineages (branches on phylogenetic trees). And if species are not individuals, then what are they? Again there are several options, e.g. collections of organisms (Ruse, 1987; Mahner & Bunge, 1997) or groups of populations (as in Mayr's *Biological Species*

Concept; cf. Boyd, 1989). On this level as well the issue has more than two horns and more than one may simultaneously be right.

The homonymic nature of the term 'species' manifests itself in at least two ways. Firstly, 'species' is used by biologists to denote both the dynamic units of evolution and the static units of biodiversity (Lidén and Oxelman, 1989; Ereshefsky, 1991; 1992; Mahner & Bunge, 1997). The architects of the Modern Synthesis emphasized the dynamic nature of species: "(…) the taxonomic categories in general, and species in particular, are not static but dynamic units." (Dobzhansky, 1935); and:

> "The species is (…) an ecological unit which, regardless of the individuals composing it interacts as a unit with other species (…). Species are the real units of evolution, they are the entities which specialize, which become adapted, or which shift their adaptation." (Mayr, 1969).

From this dynamic perspective species are composite entities that actively participate in evolutionary processes and interact as cohesive wholes with their environment and the entities therein, similarly to soccer teams participating in matches and tournaments ('interactors': Hull, 1980). Recently Gould (2002: 703ff.) extensively discussed and defended this perspective on species.

By contrast, units of biodiversity are static entities resulting from rather than participating in evolutionary processes: "Taxa (including species) are (…) atemporal components of a historical pattern. They are the products of evolution, not its determinants." (Lidén and Oxelman, 1989); and: "(…) species are generally considered to be products of evolution (lineages), but not the units participating in processes." (Kluge, 1990). Understood in this manner species constitute the building blocks of the 'tree of life' that phylogenetic systematics investigates. 'Unit of evolution' and 'unit of biodiversity' in the sense above are both individual-concepts, i.e. concepts associated with entities rather than classes. The fundamental difference between these two types of entities becomes clear when considering the allocation of organisms from the past: whereas dead organisms no longer constitute parts of any coherent entity partaking in evolutionary processes, they still belong to some branch on the tree of life.

Secondly, biological science consists of several distinct (sometimes partly overlapping) research contexts like ecology, ethology and phylogenetic systematics, all employing the concept of species in investigating their own particular kinds of questions. Since the demands posed on this concept generally are incompatible between different research contexts, no single concept will suit all contexts of biological research (Kitcher,

1984; Kornet, 1993; Shaw, 1998). The term 'species' is thus best understood as the common denominator for a number of distinct scientific concepts, each tailored to the idiosyncratic demands of a particular research context. In some cases these concepts will be individual-concepts, in others class-concepts. Many discussions of the ontology of species consider only one context, resulting in divergent conclusions: Ruse (1987) analyzed evolutionary biology and concluded that species are kinds, while Lidén and Oxelman (1989) considered phylogenetic systematics and decided that species are individuals. Both conclusions may well be valid within the considered research contexts, but their validity does not automatically extend beyond the boundaries of these contexts. Kitcher (1984), Falk (1988) and Dupré (1993) have made similar points.

A.2. Criticisms of Coleman & Wiley's defense

Coleman & Wiley defend the SAI-thesis by analyzing biologists' use of Latin species-denoting binomials. They start from the straightforward dichotomy discussed above: in biological discourse binomials can be understood to function as singular terms, i.e. terms denoting entities rather than classes, or as categorical terms to be analyzed as predicate expressions (2001: 500). Whereas the former entails an ontology of species as individuals (an 'objectual account' of species in Coleman & Wiley's terminology), the latter entails an ontology of species as classes whose names are interchangeable with predicate expressions that reflect the necessary and sufficient conditions for species membership (a 'predicative account' of species). My focus is now on the two main steps in Coleman & Wiley's defense. First (Section 2) they present some examples from biological practice in which binomials are used as singular terms. These examples serve to show that an objectual account of species fits some cases, but cannot rule out the possibility that other cases require a predicative account of species. In their Section 3 they attempt to rule out this possibility by refuting the so-called eliminability thesis, which says that binomials in biological discourse are "(…) substitutes for complex predicate expressions that do function as categorical terms" (2001: 506). Lacking a third option, a refutation of the eliminability thesis would directly entail that only an objectual account of species is adequate to biological practice.

Although I consider their first example, "*Fundulus nottii* is a species" (2001: 503), somewhat unfortunately chosen[36], I do not deny that cases in which binomials denote objects rather than classes are abundant in biology. Clear examples can be drawn from e.g. ecology or phylogenetic systematics. What I do dispute is that biology consists exclusively of such cases. Biology also comprises many cases in which binomials are used as class terms supporting generalized knowledge statements:

> "(…) If I have identified a fruit fly as an individual of *Drosophila melanogaster* on the basis of bristle pattern and the proportions of face and eye, I can 'predict' numerous structural and behavioral characteristics which I will find if I study other aspects of this individual." (Mayr, 1961).

Inferences from the observed properties of organisms to their unobserved properties (Mayr, 1961; 1969) or to properties of other organisms belonging to the same species (Millikan, 1999) must be ontologically founded, i.e. there must be an ontological guarantee that the organisms of one species are the same in relevant respects (Griffiths, 1999; Millikan, 1999). Whereas ontologies of species as classes automatically provide such a guarantee (due to the intensionality of class definitions – see below), ontologies of species as individuals with organisms as their parts do not, since an entity's parts need not be the same in any respect. Species-as-individuals ontologies must therefore explicitly state how such inferences are supported. No such accounts have been provided so far; moreover, ontologies of species as lineages are in principle unable to provide them[37].

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[36] It is not a regular statement within the biological body of knowledge. Rather, it is a metastatement connecting a scientific name to a level of organization at which nature is being studied. To say that *Fundulus nottii* is a species is on a par with saying that Helium is an element, i.e. that what bears that name has a role in scientific theory on a particular ontological level. Regular biological statements in which binomials function as names of individuals convey properties of and relations between actual species (e.g. genealogical history or geographical distribution). Coleman & Wiley's example does not convey any such knowledge.

[37] Griffiths' (1999) and Millikan's (1999) recent attempts to this extent illustrate why. Because of the slow evolutionary change that occurs within lineages inferences across the boundaries of subsequent lineages are supported in their accounts of species, while inferences from organisms at the beginning of a lineage to organisms at later stages of

By refuting the eliminability thesis Coleman & Wiley purport to establish that predicative accounts of species are unsuitable to scientific practice. The eliminability thesis however allows for a strong and a weak reading. In its strong reading the thesis entails that Latin binomials can be substituted by predicate expressions in all scientific statements in which they occur. In its weak reading it only implies that this can be done at least in some statements. Since they hold that species are always individuals, Coleman & Wiley must refute the eliminability thesis in its weak reading.

Coleman & Wiley attack two ways of conceptualizing binomials as disguised categorical terms: by understanding them as placeholders for predicate descriptions of organism morphology, or as placeholders for specific instances of general properties thought to define the species category (e.g., potential interbreeding or common descent). I do not discuss the latter point. Against the former conceptualization Coleman & Wiley hold that sets of organism characteristics necessary and sufficient for species membership are virtually impossible to obtain. This is however only the case if some other criterion for allocating organisms to species is already at work, i.e., if we attempt to reconcile organism morphology with a classification based on another preconception regarding species membership. Coleman & Wiley's remarks (2001: 507) on the suitability of characters for diagnosing but not for defining species taxa suggest that they argue from just such a biased perspective[38]. Organism morphology as criterion for species membership is bound to conflict with this phylogenetic perspective. Once this perspective is abandoned, however, the conflict disappears for lack of a second party to conflict with. Although morphology-based classes of organisms generally will be non-real, nominalistic classes and will show little overlap with the species used in phylogenetic systematics, this does not prevent them from being practically useful and theoretically significant classes that can support generalized knowledge statements in other contexts of biological research. Consider for example fields that address 'how'-questions rather than 'why'-questions (Mayr, 1961) by studying organisms with respect to structural similarities and classifying them according to analogies rather than homologies (e.g., functional morphology and ecology; see the discussion in Griffiths, 1999). Since not all of biological investigation rests on assuming a phylogenetic

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the same lineage are generally unsupported. But I must leave a more extensive discussion of why I think their accounts are unsuccessful for elsewhere: Chapter 5.

[38] Elsewhere Wiley (e.g., 1989) exhibits a similar phylogenetically biased viewpoint in his assertion (following Hennig) that not morphology but genealogy is "the solid base on which we construct our hypotheses" (1989).

perspective, arguments against the eliminability thesis based on phylogenetic considerations cannot serve to refute the thesis for the whole of biological science.

Another problem in this part of Coleman & Wiley's analysis is that it rests on the traditional essentialistic conception of natural kinds as classes of entities that all share a set of (usually microstructural) properties necessary and sufficient for class membership (2001: 502), an account that for many reasons fails with respect to species. This renders their analysis incapable of addressing alternative accounts of species as natural kinds, such as Boyd's (1989; 1999) account in which natural kinds are defined by the natural mechanisms underlying the repetitive co-occurrence of particular properties, rather than by these properties themselves. Hence, even if the eliminability thesis were refuted in its weak reading, this does not imply the rejection of such alternative ontologies of species as natural kinds.

A.3. Species as sets

In their Section 4 Coleman & Wiley criticize the conceptualization of species as sets. Although many of their arguments seem to indicate real problems for this understanding of species, Coleman & Wiley are misguided in thinking that their attack supports the SAI-thesis. The problem lies in the formal difference between sets, which are defined extensionally, and classes, which are defined intensionally (Mahner & Bunge, 1997; Muller, 2001). The debate on the SAI-thesis hinges on the issue whether species are classes, not whether they are sets (but see Kitcher, 1987). Both species as individuals and species as classes can be reconstructed as sets, implying that arguments for or against the view of species as sets cannot help to establish the ontological status of species as individuals or classes. Such reconstructions take place by way of *associating* an abstract set of organisms with a particular species taxon, which is different from *identifying* the taxon with the set. The reconstruction of a species as a set thus does not imply the ontological statement that this taxon *is* a set. Kornet (1993) performed this reconstruction on the prototypical example of species as individuals: Hennig's phylogenetic species defined as chunks of the genealogical network. Coleman & Wiley's argument, saying that on the interpretation of species as (extensionally defined) sets of organisms a species ceases to exist when its extension changes (2001: 511), does not hold for (intensionally defined) classes: whereas a different set becomes associated with a species when its composition changes, the species itself remains in existence. Since the reconstruction of species as sets is compatible with the interpretation of species as

individuals, judgments regarding the validity of the construction of species as sets do not reflect on the validity of the SAI-thesis.

A.4. Conclusion

Coleman & Wiley conclude that "(…) biological discourse contains an ineliminable reference to individual things called "species"" (2001: 516). Taken literally this statement, denying the eliminability thesis in its strong reading, is correct: in many cases Latin binomials indeed refer to individuals. However, this does not amount to saying that in biological science species are *always* to be conceptualized as individuals, i.e., it does not amount to the validity of the SAI-thesis for the whole of biology.

I believe the SAI-thesis is valid for some but certainly not all contexts of biological research. In their defense of the SAI-thesis Coleman & Wiley fail to take into consideration the heterogeneity of the species category. The fact that the term 'species' denotes different concepts in different contexts of biological research implies that in some contexts species might best be understood as individuals, whereas in others their proper ontology is that of classes or even natural kinds.

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Nederlandstalige samenvatting
(*Summary in Dutch*)

1. Het soortprobleem

Charles Darwin besloot zijn boek *Over het Ontstaan van Soorten* in een optimistische toon:

> "Wanneer de opvattingen die in dit boek over het ontstaan van soorten worden vertegenwoordigd (…) algemeen worden aanvaard, kunnen we vagelijk vooruitzien dat er een aanzienlijke revolutie in natuurlijke historie zal plaatsvinden. Systematici (…) zullen niet langer onafgebroken achtervolgd worden door de twijfel of deze of gene vorm in essentie een soort is. (…) De eindeloze disputen of zo'n vijftig soorten Britse bramen daadwerkelijk soorten zijn, zullen ophouden." (Darwin, 1859: 484 – eigen vertaling).

In de tijd die is verstreken sinds de publicatie van *Over het Ontstaan van Soorten* is Darwins optimisme echter onterecht gebleken: Darwiniaanse evolutie is weliswaar algemeen geaccepteerd, maar de discussies in de biologie over de juiste indeling van de organismale diversiteit in soorten gaan door zoals tevoren.

Dat deze discussies niet eens en voor altijd zijn gestopt, is in eerste instantie te wijten aan een nog steeds voortdurend gebrek aan duidelijkheid met betrekking tot een van de centrale termen in de biologische wetenschap: 'soort' ('*species*'). Ondanks het vele werk dat is verricht in pogingen tot verheldering van de aard van die dingen die biologen 'soort' noemen en van de criteria die worden gebruikt om soorten in de natuur te onderscheiden en organismen aan soorten toe te kennen, is dit gebrek aan duidelijkheid echter blijven voortbestaan. Wat in de loop der tijd bekend is geworden als 'het soortprobleem', bestaat in feite uit twee afzonderlijke – hoewel sterk met elkaar verweven – kwesties, een ontologisch en een epistemologisch van aard. In het voorliggende proefschrift ligt de nadruk eerst op de ontologische kant van het soortprobleem, alvorens wordt overgegaan tot het behandelen van de epistemologische kant ervan.

Om verschillende redenen is het belangrijk het soortprobleem vanuit het perspectief van de tegenwoordige stand van zaken in de biologische wetenschap te benaderen. Een reden heeft betrekking op de grondslagen van de biologie. Zonder dat een duidelijk inzicht bestaat in waarnaar de term 'soort' verwijst, op welke en in hoeveel verschillende wijzen de eenheden die met de naam 'soort' worden aangeduid in biologisch onderzoek functioneren en hoe deze eenheden in de praktijk kunnen worden

afgebakend, ontbreekt een essentieel onderdeel van de fundering onder de biologische wetenschap. Het leveren van bijdragen aan het oplossen van de conceptuele kant van het soortprobleem is dan ook een belangrijke taak van onderzoekers in de grondslagen van de biologie.

Een andere belangrijke reden heeft betrekking op de vooruitgang in de wetenschapsfilosofie. Filosofie van de biologie, zoals ik het vakgebied opvat, staat met een been in de biologische wetenschap en met het andere in de wetenschapsfilosofie, in die zin dat de kwesties die in de filosofie van de biologie worden behandeld directe gevolgen hebben voor beide genoemde vakgebieden. Dit is ook het geval met betrekking tot het soortprobleem. Kwesties uit de algemene wetenschapsfilosofie, zoals de aard van wetenschappelijke verklaringen en classificaties, epistemologische en ontologische kwesties met betrekking tot de notie van '*natural kinds*', de aard van individualiteit en de vraag wat voor soorten van dingen er in de wereld bestaan, kunnen alle worden benaderd door het soortprobleem als casus te gebruiken, waaruit nieuwe inzichten voor deze kwesties kunnen worden verkregen (zoals dit proefschrift onder meer laat zien).

Het werk aan het soortprobleem dat hier wordt gepresenteerd, is ook van belang in de context van de hedendaagse biodiversiteitcrisis. Geconfronteerd met het snelle uitsterven van grote delen van de Aardse biodiversiteit, wordt veel tijd en energie besteed aan het in kaart brengen van de werkelijke diversiteit van het leven op Aarde, de daadwerkelijke snelheid waarmee het uitsterven voortschrijdt en de mogelijkheden om dit uitsterven tegen te gaan. Doorgaans staat hierin de notie 'soort' centraal: biodiversiteit wordt onder andere gemeten in termen van het aantal aanwezige soorten in een bepaald gebied en soorten worden hierbij gezien als de primaire eenheden die kunnen uitsterven en daarom beschermwaardig zijn. Een beter begrip van de aard van soorten kan een directe invloed hebben op onze bevindingen aangaande de toestand van de Aardse biodiversiteit en daarmee een sturende factor vormen voor onze acties met betrekking tot de biodiversiteitcrisis.

Het voorliggende proefschrift heeft tot doel bij te dragen aan het oplossen van het soortprobleem in zijn hedendaagse vorm door twee aspecten van het probleem concreet te behandelen. Ten eerste wordt de aard van het soortprobleem onderzocht en wordt getoond dat het probleem dieper ligt dan doorgaans wordt aangenomen: wanneer wordt nagegaan wat de ontologische referent van de term '*species*' is, kan worden gezien dat niet één concept, maar meerdere onafhankelijke concepten in het geding zijn. Ten tweede wordt een van de epistemische rollen van het begrip 'soort' in de biologische wetenschap in detail uitgewerkt: de rol van '*species*' als verwijzend naar klassen van organismen waarover verklarende en voorspellende generalisaties bestaan.

De volgende paragraaf geeft een overzicht van de stappen die worden genomen bij het behandelen van deze kwesties.

2. Overzicht en samenvatting van het voorliggende proefschrift

Hoofdstuk 1 geeft een overzicht van het voorliggende proefschrift en is hier in het Nederlands weergegeven. In ***Hoofdstuk 2*** wordt een eerste verkenning van het soortprobleem ondernomen. Vanaf periodes lang voor die waarin Darwin leefde tot op de dag van vandaag heeft het soortprobleem de aandacht getrokken van biologen en filosofen. De hoeveelheid literatuur die over deze kwestie is gepubliceerd, is inmiddels tot immense proporties uitgegroeid. Maar waarom is het probleem dan niet al lang geleden opgelost? Waarom verschijnen er nog steeds elk jaar nieuwe artikelen en boeken (inclusief het voorliggende proefschrift) waarin het probleem wordt aangepakt?

Verscheidene auteurs die zich met het probleem hebben beziggehouden, hebben verschillende redenen gesuggereerd voor de hardnekkigheid van het soortprobleem. Sommigen hebben beargumenteerd dat de oplossing van het probleem wordt tegengehouden door een onterechte nadruk op de filosofische kant van de zaak en dat de beste benadering erin bestaat meer empirische gegevens te verzamelen over de organismale wereld. Anderen hebben tegengeworpen dat niet meer empirisch onderzoek, maar juist diepere filosofische analyse is vereist. Tegenover deze suggesties vertegenwoordig ik de opvatting dat noch de empirische kant van het soortprobleem noch de filosofische kwesties die het probleem met zich meebrengt de voornaamste oorzaak zijn van het voortbestaan van het probleem. Deze zijn veeleer symptomen van wat in mijn opvatting de werkelijke onderliggende reden is dat het soortprobleem tot op de dag van vandaag niet definitief is opgelost: te weten, het niet onderkennen dat de term '*species*' niet verwijst naar één enkel wetenschappelijk begrip, maar gedurende de ontwikkeling van de biologische wetenschap is gaan verwijzen naar meerdere *onafhankelijke* begrippen. Kort gezegd: in de hedendaagse biologie fungeert '*species*' als een homoniem.

Terwijl in Hoofdstuk 2 dit perspectief op het soortprobleem slechts kort wordt voorgesteld en wordt vergeleken met een andere recente suggestie in de literatuur, te weten dat '*species*' een familiegelijkenis aanduidt (in die zin dat alle daadwerkelijke soorten in verschillende opzichten op elkaar lijken, zonder dat ze alle een eigenschap gemeen hebben), wordt het in ***Hoofdstuk 3*** in detail beargumenteerd en uitgewerkt. In

dat hoofdstuk worden een epistemologische en een ontologische analyse van de term '*species*' uitgevoerd.

Wanneer de epistemische rollen van de term '*species*' in de hedendaagse biologische wetenschap worden beschouwd, kunnen drie zulke rollen worden geïdentificeerd: soorten fungeren als eenheden van taxonomische classificatie (eenheden in het algemene referentiesysteem dat biologen gebruiken om de specimina die ze bestuderen te ordenen), eenheden van generalisatie (klassen van organismen waarover verklarende en voorspellende wetenschappelijke generalisaties kunnen worden gemaakt) en eenheden van evolutie (entiteiten die deelnemen aan evolutionaire processen en evolutionaire veranderingen ondergaan). In tegenstelling tot wat veelal (en doorgaans impliciet) wordt aangenomen, bestaat er geen a priori reden waarom deze drie rollen alle door een en hetzelfde wetenschappelijke begrip moeten kunnen worden vervuld. En in feite, zoals in dit hoofdstuk wordt beargumenteerd, zijn de vereisten die deze rollen stellen aan het begrip dat ze dient te vervullen niet altijd compatibel, zodat meer dan één begrip benodigd is om al deze rollen te kunnen vervullen.

Het onderzoek dat wordt uitgevoerd in Hoofdstuk 3 naar de ontologie die behoort bij de term 'soort' toont aan dat deze term, zoals deze in de hedendaagse biologie wordt gebruikt, inderdaad naar meerdere begrippen verwijst. Gedurende de ontwikkeling van de biologische wetenschap is '*species*' gaan verwijzen naar vier verschillende soorten van referenten: samenhangende systemen van synchroon levende organismen, die als een geheel participeren in evolutionaire processen; segmenten van de fylogenetische boom van het leven op Aarde, die bestaan uit organismen uit zowel heden als verleden die onderling door middel van ouderschapsrelaties zijn verbonden; klassen van evolutionaire eenheden (klassen die als hun leden systemen van synchroon levende organismen hebben); en klassen van organismen die bepaalde gedrags- of structurele eigenschappen gemeen hebben. Deze vier typen van referent zijn ontologisch zeer verschillend, wat impliceert dat ze niet onder een enkel wetenschappelijk begrip kunnen worden vervat en dus dat vier verschillende begrippen in het soortprobleem aan de orde zijn. Kortweg: de term '*species*' zoals deze tegenwoordig wordt gebruikt, is een viervoudig homoniem dat staat voor vier onafhankelijke wetenschappelijke begrippen, elk verbonden met een bepaalde ontologische categorie.

Benadrukt moet worden dat ik niet suggereer dat alle vier begrippen *moeten* worden geïncorporeerd in het conceptuele kader van de biologische wetenschap. Veeleer presenteer ik de diagnose dat de vier begrippen die in Hoofdstuk 3 zijn geïdentificeerd *in feite* deel uitmaken van het conceptuele kader van de hedendaagse biologie. Of hun plaats in dit conceptuele kader uiteindelijk noodzakelijk zal blijken, is een empirische

kwestie en geen kwestie die door middel van conceptuele analyse behandeld kan worden.

Na te hebben laten zien wat de stand van zaken in de hedendaagse biologie is met betrekking tot de term '*species*', worden de consequenties van deze analyse getrokken voor twee ideeën die sterk van invloed zijn op het hedendaagse denken over het soortprobleem: soortenindividualisme en soortenpluralisme (eveneens in Hoofdstuk 3). Getoond wordt dat beide posities berusten op de (doorgaans impliciete) aanname dat de term '*species*' staat voor een enkel wetenschappelijk begrip (zij het in het geval van soortenpluralisme een 'paraplubegrip' dat uitgesplitst kan worden in een aantal afzonderlijke maar wel onderling verbonden sub-begrippen). Als zodanig zijn noch soortenindividualisme noch soortenpluralisme in overeenstemming met de daadwerkelijke stand van zaken in de biologische wetenschap, waarin '*species*' verwijst naar vier onafhankelijke begrippen. Mijn conclusie is daarom dat het aannemen van soortenindividualisme en/of soortenpluralisme een belemmering vormt bij pogingen het soortprobleem op te lossen.

In het bijzonder soortenindividualisme is wijd geaccepteerd onder zowel biologen als filosofen van de biologie. Het wordt ook behandeld in de ***Appendix***, waar ik laat zien dat een recent gepubliceerde verdediging van soortenindividualisme op verschillende fronten faalt.

De laatste twee hoofdstukken van het voorliggende proefschrift behandelen een van de drie rollen van soorten die zijn geïdentificeerd in Hoofdstuk 3: de rol van soorten als eenheden van generalisatie. In ***Hoofdstuk 4***, dat de opbrengst van het hier gepresenteerde werk voor de algemene wetenschapsfilosofie bevat, wordt de aard van wetenschappelijke generalisaties en klassen beschouwd. Volgens de traditionele opvatting in de wetenschapsfilosofie bestaan wetenschappelijke verklaringen en voorspellingen essentieel in het maken van goed gefundeerde generalisaties. Waargenomen overeenkomsten in de eigenschappen van verschillende entiteiten worden bijvoorbeeld verklaard door deze entiteiten te identificeren als behorend tot dezelfde '*natural kind*' en ze daarmee te vervatten onder een generalisatie van het type 'Alle (dan wel de meeste) entiteiten van soort *K* vertonen de eigenschap *p*.' Op een soortgelijke manier worden ongeobserveerde eigenschappen van entiteiten van een bepaalde soort in heden en toekomst voorspeld door middel van een generalisatie die stelt dat als een bepaalde entiteit zou behoren tot de soort *K*, deze (met hoge waarschijnlijkheid) een bepaalde eigenschap of set van eigenschappen zou vertonen. In dit hoofdstuk wordt getoond dat twee typen generalisaties benodigd zijn om de overeenkomsten te verklaren en te voorspellen die organismen vertonen in hun gedrags- en structurele eigenschappen.

De aanname is wijd verbreid dat alle wetenschappelijke verklaring en voorspelling plaatsvindt door middel van universele natuurwetten. In tegenstelling tot deze aanname tonen de overwegingen in Hoofdstuk 4 dat twee fundamenteel verschillende typen generalisaties een rol spelen in wetenschappelijke verklaring en voorspelling: deze worden hier '*law-generalizations*' en '*kind-generalizations*' genoemd. '*Law-generalizations*' hebben betrekking op toestandsveranderingen en beroepen zich niet direct op wetenschappelijke klassen; '*kind-generalizations*' hebben betrekking op de eigenschappen van materiële entiteiten en gelden over de leden van klassen van entiteiten.

Nadere beschouwing van '*kind-generalizations*' laat zien dat twee typen wetenschappelijke klassen bestaan waarover verklarende en voorspellende generalisaties gelden, die berusten op verschillende typen van onderliggende factoren: spatiotemporeel ongelimiteerde '*causal kinds*' waarover generalisaties gelden, die berusten op causale mechanismen die werken op de entiteiten die tot de betreffene klassen behoren, en spatiotemporeel gelimiteerde '*historical kinds*' waarover generalisaties gelden, die berusten op de gemeenschappelijke geschiedenis van de leden van de betreffende klassen. De aard van de factoren die onderliggend zijn aan generalisaties over de leden van '*causal kinds*' is dusdanig dat dergelijke generalisaties uitzonderingsloos kunnen zijn, maar ook uitzonderingen kunnen vertonen. Op dezelfde wijze kunnen ook generalisaties over de leden van '*historical kinds*' zowel uitzonderingsloos zijn, als ook uitzonderingen vertonen.

Uit deze resultaten volgt dat het wijdverbreide gebruik van het criterium van universaliteit om de wetenschappelijke geldigheid van verklaringen en de wetenschappelijke status van vakgebieden te evalueren, niet juist is. Terwijl dit criterium toepasbaar is op verklaringen in termen van '*law-generalizations*', is het gebruik ervan misplaatst met betrekking tot verklaringen in termen van '*kind-generalizations*'. Verklaringen en voorspellingen van overeenkomsten in de eigenschappen van materiële entiteiten berusten op '*kind-generalizations*' die niet geëvalueerd dienen te worden in termen van universaliteit. Dit betekent dat de opvatting dat geldige wetenschappelijke verklaringen slechts kunnen berusten op uitzonderingsloze, spatiotemporeel ongelimiteerde generalisaties, niet juist is.

Een gevolg hiervan is dat de wetenschappelijke status van de biologie in een nieuw licht gezien moet worden. Biologie wordt in het algemeen geplaatst tegenover de fysische wetenschappen met betrekking tot verklarende en voorspellende inhoud. Terwijl de fysische wetenschappen betrekking hebben op universele generalisaties (natuurwetten) die kunnen dienen als de bases voor geldige wetenschappelijke

verklaringen en voorspellingen, zijn de generalisaties van biologie niet-universeel en daarom ongeschikt om wetenschappelijke verklaringen en voorspellingen te ondersteunen. Biologie, zo wordt vervolgens geconcludeerd, kan vanuit zichzelf geen eigen verklaringen produceren, maar maakt gebruik van verklaringen en voorspellingen die berusten op de wetten uit de fysische wetenschappen. Deze redenering kan nu als onjuist ontmaskerd worden: biologie heeft wel degelijk de beschikking over haar eigen verklarende en voorspellende generalisaties, die echter niet moeten worden gemeten langs de maatstaf van universaliteit.

Hoofdstuk 4 vormt een voorloper van ***Hoofdstuk 5***, waarin de rol van soorten als eenheden van generalisatie in de biologische wetenschap wordt beschouwd. De wetenschapsfilosofen Paul Griffiths en Ruth Millikan hebben recentelijk betoogd dat soorten, opgevat als segmenten van de fylogenetische boom van het leven op Aarde, kunnen en moeten worden geïnterpreteerd als wetenschappelijke klassen waarover verklarende en voorspellende generalisaties gelden. Contra de suggestie die door Griffiths naar voren is gebracht, beargumenteer ik dat de ontologie van soorten als segmenten van een fylogenetische boom intrinsiek in tegenspraak is met elke mogelijke opvatting van soorten als '*natural kinds*' (die in de theorie die in dit proefschrift wordt ontwikkeld een ondercategorie vormen van '*causal kinds*'). Daarnaast wordt in dit hoofdstuk getoond dat niet alle typen van segmenten van fylogenetische bomen op het soortniveau opgevat kunnen worden als '*historical kinds*' en dat een dergelijke opvatting slechts mogelijk is onder een bepaalde definitie van soorten als segmenten van fylogenetische bomen, te weten het *Composite Species Concept*.

3. Slotbemerking

De hoofdstukken in het voorliggende proefschrift zijn geschreven in verschillende stadia van lopend onderzoek. Ze weerspiegelen daardoor veranderingen die mijn denken over het soortprobleem heeft ondergaan. Een voorbeeld is het volgende. Terwijl ik in Hoofdstuk 3 aanneem dat de rol van soorten als eenheden van generalisatie een ontologie van soorten als klassen vooronderstelt, laat ik in Hoofdstuk 5 zien dat deze rol van soorten ook compatibel is met een ontologie van soorten als spatiotemporeel gelimiteerde entiteiten: onder het *Composite Species Concept* kunnen segmenten van fylogenetische bomen worden opgevat als '*historical kinds*' (eenheden waarover historische generalisaties gelden). Dit resultaat leidt op zijn beurt tot een ander resultaat dat niet is geanticipeerd in hoofdstuk 3. In dat hoofdstuk is beargumenteerd dat meer dan

een begrip benodigd is om de drie epistemische rollen van soorten te kunnen vervullen. Het *Composite Species Concept* was oorspronkelijk ontwikkeld als definitie van soorten als eenheden van classificatie, maar naar nu blijkt, definieert het *Composite Species Concept* entiteiten die twee van de epistemische rollen van soorten simultaan kunnen vervullen: die van eenheden van historische generalisatie en van eenheden van classificatie.

Referentie

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1997-1998:	store manager, Kooyker Ginsberg booksellers, campus store Technical University Delft, Delft (The Netherlands).
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Publications:

refereed journal articles:

1. 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.
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2. *Acta Biotheoretica: An international journal on the mathematical and philosophical foundations of biological and biomedical science*, Volumes 50 (2002) – present (journal published by Kluwer Academic Publishers, from 2005 onward published by Springer).

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1. Reydon, T.A.C. & Kornet, D.J. (2004). Soorten in de systematische biologie. In: Diekmann, O., Heesterbeek, J.A.P. & Metz, J.A.J. (Eds): *De Wiskundige Kat, de Biologische Muis en de Jacht op Inzicht: Verkenningen op het Grensvlak van Wiskunde en Biologie*, Utrecht: Epsilon, pp. 199-218.

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1. Reydon, T.A.C. (2002). De kruisbestuiving van biologie en filosofie: over soorten en *natural kinds*. In: Bartsch, R., Beentjes, R., De Bruin, B. & Van der Leeuw, K. (Eds): *Filosofie & Empirie: Handelingen van de 24e Nederlands-Vlaamse Filosofiedag*, Amsterdam: Faculteit der Geesteswetenschappen, Universiteit van Amsterdam, pp. 177-185.
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7. Reydon, T.A.C. (2003). Book Review of *Quantum Theory: A Very Short Introduction* by John Polkinghorne. *Contemporary Physics* 44: 465-466.
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4. Anon. (1999). *Over de Organisatie van Publieke Debatten* (On the Organization of Public Debates), report written for the Dutch Minister of Health, Welfare & Sports (*VWS*), Den Haag: Ministerie van Volksgezondheid, Welzijn en Sport, 65 pp.
5. Anon. (1999). *Tweede Voortgangsrapportage Biotechnologie en Levensmiddelen* (Second Progress Report on Biotechnology and Foodstuffs), report presented to the Dutch Parliament by the Ministers of Health, Welfare & Sports (*VWS*) and Agriculture, Nature and Fisheries (*LNV*), *Tweede Kamer der Staten Generaal, vergaderjaar 1998-1999*, 26 407, nr. 2, pp. 13-35.

Presentations of Ph.D.-research:

Parts of the work contained in this Ph.D.-dissertation have been presented in talks at various national and international meetings: the XIXth meeting of the Willi Hennig Society (Leiden, May/June 2000), the 22nd and 24th Dutch-Flemish Philosophy Day (*Nederlands-Vlaamse Filosofiedag*) (Leiden, October 2000 and Amsterdam, November 2002); the 26th, 27th and 28th Annual Philosophy of Science Conference (Dubrovnik, April 2000, April 2001 and April 2002); the 2001 and 2003 meetings of the International Society for the History, Philosophy, and Social Studies of Biology (Hamden (Conn.), July 2001 and Vienna, July 2003); and the 12th International Congress of Logic, Methodology and Philosophy of Science (Oviedo, August 2003). A poster was presented

at the conference 'Contextualizing the Genome: The Role of Epigenetics in Genetics, Development and Evolution' (Ghent, November 2001). Part of the Ph.D-training was participation in three summer schools: the 3rd and 4th Kira Institute summer schools at Amherst College (Amherst (Mass.), 2000 and 2001) and the 6th Erasmus Course in Systematic Biology at the University of Florence (Florence, 2001).