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SPECIES PLURALISM

By

John Alan Holmes

A DISSERTATION

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ABSTRACT

SPECIES PLURALISM

By

John Alan Holmes

The central aim of the dissertation is to recommend an account of species pluralism that addresses a wide range of biological situations without resulting in theoretical tension between the pluralistic parts of the account. Species pluralism holds that more than one species concept is necessary in order to adequately address the wide variety of grouping phenomena identifiable as species. Proper assessment of an account of species pluralism requires assessing the number of biological situations the account covers as well as determining whether the account fits within a single theoretical framework. An account of species pluralism that includes a large number of species concepts appears to have the benefit of covering a large of number of biological situations. However, such an account also runs the risk of not fitting neatly within a single theoretical framework. An account that includes species concepts from different theoretical frameworks is said to give rise to disciplinary discord.

This dissertation will defend the claim that species pluralism is necessary in order to do biology properly. In particular, an account of species pluralism offered by Kitcher (1984a, 1984b, 1987, 1989) will be defended. Kitcher suggests that species pluralism ought to include neo-Darwinian species concepts as well as non-Darwinian species concepts. Although Kitcher's account runs the risk of disciplinary discord, arguments will be presented which suggest that both types of species concepts can be integrated within a single theoretical framework. Some of the ways in which the species concepts might be integrated involve relaxing theoretical jargon, re-conceptualizing the types of entities picked out as species by the various species concepts so that they fit into a single hierarchy, and developing research projects, as well as institutional organizations, that are acceptable to both neo-Darwinians and non-Darwinians.

for Gunnar

may you question the status quo as appropriate

ACKNOWLEDGMENTS

My completion of this work is as much a testament to other's abilities as it is to my own. As a result, I would like to thank a number of people who have supported my effort to complete this work throughout the past eight years. To my mother, father, and my brother Ted I say thank you. Your continual support has helped get me over some difficult humps during this eight year journey. I will not forget all the encouraging words all three of you have offered me. Ted, I owe you a special thank you for allowing me to vent my frustrations upon you whenever I saw fit during the past eight years. To my advisor Fred Gifford I say thank you as well. Your patience, insightful commentary, and trust have allowed me to finish this dissertation largely on my own terms. I would also like to thank my little boy Gunnar for bringing joy to my life during the past six years while I was not busy writing. In addition, I would like to thank the members of my committee for being so patient and flexible, the Department of Philosophy for granting me a Dissertation Completion Fellowship, and the Department of Horticulture for spurring my latent interest in biology. Finally, I would like to thank three friends; H. Skott Brill, Matthew Stock, and Christine Parks. H. Skott, I will always cherish the moments we spent on rivers recuperating from our graduate school studies. Matt, you have given me a certain physical drive I never had before I met you. Christine, thank you for helping me through an extremely difficult time in my life. You have all helped me uncover (and rediscover) who I am and for this I am forever grateful.

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INTRODUCTION

Present day taxonomists and evolutionary biologists have not been able to reach consensus on what counts as a species. Some hold that a species is a group of organisms united by reproductive forces. Others hold that a species is a group of organisms united by selective forces. Still others hold that a species is a group of organisms which share at least one unique characteristic and have descended from a single common ancestor. Indeed, Ereshefsky (1992) distinguishes nine different accounts of what a species is. This disagreement among taxonomists and evolutionary biologists is disturbing since the species concept is a fundamental concept of biological taxonomy and evolutionary biology. Perhaps further empirical investigation will bring consensus, but this does not seem likely.

An increasingly popular response to this lack of consensus is species pluralism. In its basic form, species pluralism is the idea that there is no single best definition of species; given the vast amount of diverse biological situations and the complexity of biological processes, evolutionary biology requires more than one species concept. Some apparent benefits of species pluralism are that it (1) satisfies many different theoretical interests by providing a more complete causal account of species and (2) contributes to scientific progress by providing answers to previously unanswered questions about the nature of species. However, a problem facing any account of species pluralism concerns deciding what species concepts ought to be recognized. Advocates of species pluralism will want to aim for a pluralism that is reasonably diverse yet still theoretically uniform.

If species pluralism is limited to a small set of species concepts in order to improve theoretical manageability, it may fail to adequately address the wide array of biological situations and causal processes. If species pluralism includes a wide variety of species concepts, there is a worry that the various species concepts might not fit neatly within a single theoretical framework.

The primary aim of this dissertation is to suggest an appropriate account of species pluralism for use within contemporary biology; an account that incorporates a wide variety of theoretical interests while still remaining theoretically manageable. We will focus on the question of whether an acceptable account of species pluralism needs to be solely neo-Darwinian in nature. In recent years, certain developmental biologists, Process Structuralists, have offered a brazen critique of neo-Darwinian biology. Of particular interest in this dissertation are the ideas of these Process Structuralists and what impact their ideas of species should have, if any, on the nature of species pluralism. Although a solely neo-Darwinian account of species pluralism appears less troubled by issues of theoretical manageability, such an account still faces important challenges. Ereshefsky (1995) has noted these challenges and attempted to address them. This dissertation aims to re-examine some of these challenges by considering to what degree the ideas of non-Darwinians such as the Process Structuralists ought to be incorporated into an acceptable account of species pluralism.

I. Recent Changes in Evolutionary Biology

Neo-Darwinism has been the prevailing theoretical framework for evolutionary biology throughout the last 100 years. Yet, modern biology's understanding and application of neo-Darwinism has changed over the past 25 years. Part of this change is seen in the growing number of neo-Darwinians who accept the *species-as-individuals thesis* and in the increased interest in species pluralism. We will examine the species-as-individuals thesis and species pluralism in a moment, but before this we need to briefly examine the nature of neo-Darwinism.

Most biologists nowadays are what we might call neo-Darwinians. But just what is neo-Darwinism? Mayr (1988) offers a brief synopsis of Darwinism which helps shed some light on *neo*-Darwinism. He suggests there are five basic tenets of Darwinism; the theory of evolution, the theory of common descent, the theory of gradualism, the theory of the multiplication of species, and the theory of natural selection. The label neo-Darwinism arose after the Modern Synthesis which refers to the coupling of the genetic theory of inheritance with Darwin's theory of natural selection. Neo-Darwinians, then, embrace the theory of natural selection and they further suppose that the theory of genetic inheritance underlies the mechanism of natural selection. Furthermore, neo-Darwinians hold that the five tenets are fully able to explain both microevolutionary changes (i.e. changes within a species) as well as macroevolutionary changes (i.e. changes between species and between higher taxa).

Species-as-individuals Thesis

Up until the middle 1960's, most biologists thought of species as classes of organisms. Critical examination of Darwinism by Hull (1965) and Ghiselin (1966) gave birth to the idea that conceiving of species as classes of organisms was flawed. Over the years since, Hull and Ghiselin have been the predominant advocates for the species-as-individuals thesis.

The species-as-individuals thesis holds that from an ontological perspective species are actually individuals as opposed to classes. Support for this thesis will be described more fully in Chapter 3, but briefly the support stems mainly from the idea that the theory of common descent and theory of evolution require that species consist of spatio-temporally connected parts (i.e. organisms). Acceptance of the thesis would appear to require reconceptualization of the current taxonomic scheme. This is because a traditional classificatory scheme classifies organisms into species which are viewed as natural kind classes as opposed to hierarchically ordering organisms in light of viewing them as being part of a larger individual. In turn, it would appear that a reconceptualization of the explanatory nature of the biological taxonomic hierarchy is necessary as well. If species turned out to be individuals, the taxonomic hierarchy would appear to function more like a rather large narrative description instead of as a nested hierarchy subject to general laws from which consequences and predictions are inferred.

Species Pluralism

Traditionally, biologists have embraced species monism. Species monism is the position that there is only one legitimate approach to defining species. Most biologists in the 20th century have been species monists, content with Ernst Mayr's biological species concept which defines a species as "a group of interbreeding natural populations that is reproductively isolated from other such groups."[1] However, the deference toward species monism is shifting slightly in biology. As noted earlier, there is not a clear consensus about which species definition is the correct one. The most widely accepted species definition, the biological species concept, has faced difficulties ever since its introduction by Mayr a little more than half a century ago. The inability of advocates of the biological species concept to adequately respond to these difficulties has prompted some biologists to advance alternative species definitions. Currently, biology contains a number of different species definitions each of which has a seemingly unique and important role.

In light of there being a number of different and seemingly important species definitions, some neo-Darwinians have embraced species *pluralism* instead of species monism. Basically, species pluralism is the position that there is no single best definition of species that will address all the diverse situations within evolutionary biology. Advocates of various species concepts each believe their respective concept offers the best causal account of the processes that maintain species. As a result, species pluralists advocate the use of more than one species definition within biology at any give time. The upshot of this is that species pluralism is not wedded to the idea that each group of organisms labeled as species must have the same underlying causal account. It is quite possible that a given biological situation may elicit the use of more than one causal account when identifying species. Furthermore, some accounts of species pluralism allow for potential cross classification to occur within a given group of organisms. This means

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[1] Mayr and Ashlock (1991, p. 26)

that for any set of organisms it is possible, when deploying more than one species definition upon that set of organisms, for different species definitions to group the organisms into two or more groups that fail to have the same organism membership. This type of cross classification results from the use of two or more species concepts that utilize different causal accounts to identify species.

In this dissertation, we will be particularly interested in examining what types of species concepts ought to be included in an account of species pluralism. Pluralism within any discipline elicits questions regarding the nature of legitimate pluralistic explanations, appropriate pluralistic methodology, and theoretical compatibility of the various pluralistic parts. We will address these same sorts of questions as we look more closely at species pluralism. But again, the main question to be addressed in this dissertation concerns just how pluralistic species pluralism can be while still being being theoretically manageable.

II. How Pluralistic Should Species Pluralism Be?

Ereshefsky (1992, 1995) asserts that species pluralism ought only contain species concepts that are consistent with neo-Darwinism. Although most biologists are neo-Darwinians, there are a number of biologists who reject the Darwinian notion that the mechanism of natural selection, by itself, adequately explains evolutionary events. In particular, *developmental* biologists argue that the mechanism of natural selection fails to adequately consider the impact of developmental constraints on the outcome of a species. They argue that developmental constraints ought to be investigated as a causal factor whenever it appears that natural selection is unable to give a satisfactory account of m

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microevolutionary changes. Most developmentalists concede, however, that natural selection and common descent are the primary causal factors of microevolutionary changes within species and macroevolutionary changes among the current phylogeny of species. In light of these concessions, the account of evolution offered by these developmentalists appears consistent with neo-Darwinism.

Of particular interest to the themes in this dissertation, however, is a rather radical group of developmentalists who have been dubbed Process Structuralists. This group of rather staunch developmentalists wholly reject the idea that natural selection is the primary explanatory factor behind microevolution and macroevolution, yet they nonetheless embrace the idea of evolutionary change. They merely cite a different causal mechanism for the change; namely, they suggest that developmental constraints are the primary causal factors of the characters exhibited by organisms and of the current phylogeny of species.

The Process Structuralist account of evolutionary change is quite involved and uses unfamiliar jargon. Although the following brief exposition of the Process Structuralist account will sound a bit foreign, for the purposes of the Introduction it is important to get a sense of what such an account entails. A detailed analysis of the account, including a interpretation of the jargon, will be provided in Chapter 2.

With regard to macroevolutionary events, Process Structuralists argue that species and higher taxa are products of what they identify as "the rational processes of *morphogenetic fields*" which underlie the development of all organisms.[2] They hold that universal laws of morphological development govern the development of species and other higher taxa.

Although the Process Structuralist account is non-Darwinian, it is nonetheless evolutionary. Evolutionary change just has a different causal mechanism on this account; Darwin's mechanisms of natural selection and common descent are replaced by a mechanism in the form of various transformational morphogenetic fields. Species are said to be maintained by developmental pathways. Speciation occurs when a morphogenetic field goes through a transformation process during reproduction or embryonic development and ultimately produces a related but slightly different form in the progeny. The various morphogenetic fields and the resulting natural kinds (i.e. species) they produce do not have to match the terminal taxa which result from an examination of the genealogical record. Process Structuralists admit that it is still possible to trace the genealogical record and identify various genealogical taxa, but they argue such genealogical taxa fail to have any real explanatory value in light of the underlying morphogenetic fields which are said to be ultimately responsible for the world's organic diversity.[3]

Determining which species concepts ought to be included in an account of species pluralism is a difficult task. Leave aside the Process Structuralists for the moment and

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[2] "Rational" does not mean intensional to advocates of Process Structuralism, rather it means something like "objective" or "universal."

[3] Whether the factual claims made by Process Structuralism are true is admittedly controversial. We will address this issue when we consider the full account of Process Structuralism in Chapter 2.

consider such a task solely within a neo-Darwinian context. As we will see, there would appear to be at least four possible neo-Darwinian species concepts. Hence, there would appear to be at least four separate accounts for why a given group of organisms is labeled as a species reflected by the following concepts; the biological species concept, the ecological species concept, the evolutionary species concept, and the phylogenetic species concept. The question facing a neo-Darwinian account of species pluralism is whether these various accounts of species can be unified under a single taxonomic hierarchy. If so, then it would appear that a neo-Darwinian account of species pluralism does not embrace species concepts that are in theoretical conflict. Accounts of species pluralism that include a wide array of species concepts run the risk of what we will call *disciplinary discord.* We will examine the nature of disciplinary discord more closely in Chapter 4, but for now we will briefly define disciplinary discord as the use of two (or more) inconsistent or possibly incommensurable explanatory accounts to account for phenomena in a given domain.

We will examine two accounts of species pluralism, one offered by Ereshefsky (1992, 1995) and another offered by Kitcher (1984a, 1984b, 1989). Ereshefsky argues that species pluralism does not give rise to disciplinary discord in evolutionary biology. He argues this because he believes all neo-Darwinian accounts of species share the idea that species are in some sense individuals even if they are individuated differently. Ereshefsky argues that the idea that species are individuals helps to theoretically unify the neo-Darwinian accounts of species. Kitcher argues that structural based species concepts, such as the one offered by Process Structuralists, may well have a place alongside neo-Darwinian species concepts in an account of species pluralism. Assuming that Process Structuralism is tenable, it would appear that Kitcher needs to address how to deal with the possibility of disciplinary discord between neo-Darwinian and Process Structuralist species concepts. This is because Process Structuralists argue that biology ought to be modeled after chemistry and physics. As a result, they argue biology ought to pursue the discovery of the universal laws of morphological development through the classification of species as natural kinds. Such a project would appear to be in conflict and even incommensurable with the neo-Darwinian approach to biological taxonomy and species.

Briefly, this conflict/incommensurability can be seen at a couple of different levels. For example, as noted already, neo-Darwinians appear to be committed to some version of the species-as-individuals thesis which holds that species are not classes but rather individual wholes with organisms as parts. As a result, neo-Darwinians suggest that an account of species ought to focus on developing lengthy historical narratives of each species much like the biographies of people. Process Structuralists, on the other hand, reject an individualist approach in favor of a more traditional, natural kinds approach to species that utilizes intensional definitions. As a result, Process Structuralists suggest that an account of species ought to focus on developing lawlike generalizations about each species. The consequences of this difference are borne out on occasions when a Process Structuralist account of evolution suggests taxonomists ought to group organisms against the grain of the genealogical record in order to properly capture an important morphogenetic field within a lawlike generalization. If the same morphogenetic field underlies two different groups of organisms which are not connected via common ancestry, a taxonomist with Process Structuralist leanings would group organisms into one species according to the morphogenetic field, instead of into two species according to the criterion of genealogy. In light of these differences, it would appear that a neo-Darwinian account of species and taxonomy is somewhat incompatible with a Process Structuralist account. The nature of this disciplinary discord and what to do about it are of central interest in this dissertation.

III. A Brief Overview of the Chapters

As mentioned already, the main purpose of this dissertation is to explore what a legitimate account of species pluralism ought to look like. Although pluralism has been a popular topic among philosophers of biology over the past 25 years[4], the question of how contemporary evolutionary biology ought to embrace *species* pluralism still begs to be answered. This dissertation takes a somewhat new approach to the species pluralism debate by critically examining whether an account of species pluralism which encompasses both neo-Darwinian species concepts and structural based species concepts is tenable. In so doing, it is hoped that the dissertation will lay grounds for a rather robust account of species pluralism which, on the one hand, provides a complete account of the nature of species, and, on the other hand, avoids the problem of disciplinary discord.

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[4] See Ereshefsky's 1992 anthology *The Units of Evolution*.

In Chapter 1 we will review the two main roles the species have had within biology since the advent of Darwinism. Briefly, these roles are as follows. First, species have functioned as a basal taxonomic unit, and second, species have functioned as units of evolution. Understanding these roles and how they occasionally intertwine is important in order to properly understand the scope problem which faces any account of species pluralism.

In Chapter 2 we will review the problem of defining species. We will review this problem primarily from a neo-Darwinian perspective, although we will examine non-Darwinian species definitions near the end of the chapter. Not surprisingly, we will find that this definitional problem has been rather intractable. We will begin the chapter by examining a phenetic approach to species and the serious flaws that are associated with any attempt to develop a theory-neutral species concept. From here we will review four neo-Darwinian species concepts; the biological species concept, the ecological species concept, the evolutionary species concept, and the phylogenetic species concept. We will tentatively conclude that each of these four concepts has its own important advantages and that no clear answer can be given regarding which species concept is best. We will end the chapter by briefly examining some non-Darwinian species concepts. In particular, we will examine a genetic approach and a Process Structuralist approach. We will conclude the chapter by offering some reasons in favor of species pluralism.

In Chapter 3 we will review the philosophical problem surrounding the ontology of species. Consideration of this problem will provide a foundation for understanding why disciplinary discord is an especially difficult problem for an account of species

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pluralism that includes both neo-Darwinian and non-Darwinian species concepts. We will review the now popular neo-Darwinian position that species are actually individuals instead of classes. We will identify and critically examine two specific arguments in favor of this position; the *No Lawlike Generalizations* argument and the *Evolutionary Term* argument. We will conclude that from a neo-Darwinian perspective it makes the most sense to say species are individuals. However, we will find that species might plausibly be viewed as sets of organisms, even from a neo-Darwinian point of view, in certain situations. Furthermore, we will find that a non-Darwinian perspective, such as a Process Structuralist approach, views species as sets or classes of organisms. We will conclude the chapter by arguing that the ontology of species is largely dependent upon one's theoretical leanings.

In Chapter 4 we will critically examine species pluralism. We will examine an account of species pluralism offered by Ereshefsky (1992, 1995) and one offered by Kitcher (1984a, 1984b, 1989). Although species pluralism is a more plausible position than species monism, we will find that any account of species pluralism faces some serious objections. We will examine and assess four objections to species pluralism; the communication objection, the inconsistency objection, the anything goes objection, and the single approach objection. Ereshefsky offers replies to the first three objections, but his reply to the anything goes objection leaves something to be desired. Furthermore, we will find that Kitcher's account of species pluralism appears to suffer from disciplinary discord. We will consider ways of dealing with theorertical discord in a Kitcherian account of species pluralism. Finding ways to ease this discord is important since a

Kitcherian account of species pluralism incorporates a wider set of biological interests. We will hold that an account of species pluralism incorporating a wider set of biological interests is to be preferred over any other account incorporating a less wide set of biological interests, as long as the account incorporating the wider set of biological interests adequately deals with disciplinary discord. We will find that the discord facing a Kitcherian account of species pluralism is similar to the discord described by Gould and Lewontin (1978) except that species pluralism deals with macroevolutionary phenomena instead of microevolutionary phenomena. We will argue that the discord within Kitcher's account might be alleviated by broadening the scope of the conceptual tools used by both neo-Darwinians and Process Structuralist as well as attempting to develop some interdisciplinary research programs and institutional organizations.

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CHAPTER 1: PRELIMINARY THOUGHTS ABOUT SPECIES

Consider the difference between trying to explain the occurrence of groups of organisms called species versus using a species concept to explain some biological phenomenon. In the former instance, the label 'species' is employed when biologists see a significant grouping phenomena involving organisms. Evolutionary biologists view these various grouping phenomena as *explananda* and then develop an account of what caused these groups to come about.

Although we might be tempted to say that particular species are *explananda*, this temptation ought to be resisted. As we will see, the use of a particular species label presupposes that an account of what a species is has been developed. It is better to view the various grouping phenomena which are ultimately labeled as species as the *explananda* and the species concept or definition used to label the various grouping phenomena as the *explanans*. We will talk more about what leads evolutionary biologists to label entities as species in the next chapter. But before we address such causal matters it is important to first have an understanding of the way in which the species concept functions as an *explanans*.

I. Why Label and Define Particular Groups of Organisms?

In order to properly understand the function of the species concept, it is important to distinguish between microevolutionary phenomena and macroevolutionary phenomena. Microevolutionary phenomena are identified as evolutionary changes within particular species. For example, evolutionary biologists interested in microevolution m

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might attempt to identify adaptations caused by natural selection within a species. Macroevolutionary phenomena are identified as evolutionary changes at or above the species level. For example, evolutionary biologists interested in macroevolution might attempt to account for species staying in stasis or the development of new species. The species concept is an important part of both microevolutionary and macroevolutionary studies. In this dissertation, we will primarily be interested in macroevolutionary phenomena and the role the species concept plays in relation to such phenomena.

A species concept needs to cite some underlying causal mechanism that explains the various groups of organisms that evolutionary biologists end up labeling as species. If there is no causal mechanism cited, the species concept fails to be of any scientific use. Regardless of one's theoretical commitments then, the trick for evolutionary biologists interested in defining the general term 'species' is to develop a definition of 'species' that does not stop with the mere perceived similarities between organisms.[1] The standard *modus operandi* for evolutionary biologists has been to use perceived similarities between a group of organisms to develop a preliminary species *diagnosis* and then test for underlying causal factors which can be said to maintain the perceived similarities among that group of organisms. Which type of tests are performed depends upon what causal factor is believed to underlie the perceived similarities of the group. The identification of

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[1] In Chapter 2 we will critically examine an approach to defining species that stops at perceived similarities. This is the phenetic approach to defining species. We will see that such an approach is conceptually flawed.

some causal force which is said to maintain groups of organisms over time is central to any account of species.[2]

Unfortunately for evolutionary biologists, developing a species concept which accounts for groups of organisms that are maintained over time is a rather difficult activity. The activity poses additional explanatory problems when compared to other scientific phenomena (such as the death of an animal, the birth of an offspring, or the movement of a star across the night sky). In the first place, it is hard to actually see a whole species. Typically, scientists are motivated to offer an explanation of some phenomenon because they regularly see the phenomenon. For example, we might see a star move across the night sky on a regular interval and then wonder how such movement occurs or we might encounter a series of dead animals and wonder how they met their demise. In these rather circumscribed examples, the whole phenomenon is clearly visible to us. With species, however, biologists do not clearly see the whole phenomenon they are trying to explain. For the most part biologists must be satisfied with seeing parts or aspects of species. This is because species are spread out over distances and time; the entire phenomenon is not restricted to one singly observable place and time.

Certainly we can see portions of a given species. When we see a cat, we are seeing a portion of *Felis domestica*; we do not see the whole species *Felis domestica*. Also, we can see groupings of plants and animals in the wild, but we do not clearly see a whole

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[2] Other related interests involve the identification of causal forces which result in the production or extinction of species. We will be concerned primarily with what maintains the groups of organisms biologists label as species. As we will see in Chapter 4, Griffiths (1996) describes the phenomenon of the maintenance of species as "phylogenetic inertia."

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species. It is incredibly difficult to see a whole species. Imagine trying to gather all the domestic cats together so that one could see all of *Felis domestica*. Even if we killed all but five domestic cats and then gathered those five together in the same room, we still would not be seeing the whole of *Felis domestica*. Consider the long history of domestic cats that have lived prior to the hypothetical act of mass killing. Presumably, we would still need to explain the occurrence of those historical cats as well as the occurrence of the cats that are currently alive.

Even the limiting case of "catching" the birth of a new species by witnessing the production of one novel offspring would not be a clear cut example of observing a whole species. As time goes on, more offspring will be produced that are part of the new species. Yet, since we cannot see these future offspring when we are examining the current members or parts, we cannot clearly say that we can see the whole species.

Another difficulty that species present for evolutionary biologists is that it is difficult to see any actions, movements, or behaviors made by species. As a comparison, suppose we want to explain why our friend acted the way he did when he yelped while walking bare foot on the sidewalk. Here we have a perceivable act; the act of our friend yelping. Given that we are properly situated, we will be able to see the entire act. We can then proceed to offer explanations of the act; maybe our friend stepped on a piece of glass or maybe the sidewalk was hot. Consider the case of species; what comparable perceivable behaviors do species engage in? For the most part, species stay in stasis. This is exactly the reason why evolutionary biologists feel compelled to identify them as species. We might say that species evolve or species go extinct. However, neither of thes

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these "behaviors" is any easier for evolutionary biologists to see. The reason would appear to be because having a clear view of a whole species is very difficult if not impossible.

In light of these points, we might ask then, 'what leads biologists to name species?' It appears that two distinct but related phenomena involving organisms lead biologists to name species. First, some groups of organisms have distinct and recognizable boundaries (usually indicated by some perceived, shared properties). In other words, some groups of organisms are perceived to be relatively discrete. We may not be able to see all the members or parts of a species, but we see enough members or parts in discrete groups that we become interested in explaining this phenomenon of discreteness. Second, these discrete groups have a certain degree of stability over a rather extended period of time; they do not just appear and disappear in a moment's notice. Hence, even without diving into specific causal details, it would appear that we can safely say groups of organisms that are discrete and exhibit extended stability are chosen by evolutionary biologists to be labeled as species. In the next chapter we will examine some of the specific causal accounts offered by biologists to explain the groups of organisms labeled as species.

II. Two Main Roles of Species in Contemporary Biology

In order to get a better sense of the function of a species definition it will be helpful to examine two main roles the term 'species' is said to fulfill within biology.[3] On

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[3] This distinction is gleaned from Ereshefsky (1992).

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the one hand, it picks out a basal taxonomic unit. On the other hand, it picks out the fundamental unit of evolution.

Species as Basal Taxonomic Units

To say that species, in the class-oriented sense of this term, function as the basal taxonomic units within the taxonomic hierarchy in biology is to say that species delimit the least inclusive groupings of organisms recognized by taxonomists. All taxa above the species level form the class of *higher taxa*. Any other groupings below the species level are deemed unworthy of recognition primarily because such groupings are thought to be biologically uninteresting and therefore unworthy of taxonomic distinction. An example of such an unworthy taxonomic grouping might be race.

One of the most pressing questions facing taxonomists over the last 100 years concerns what the definition of the taxonomic term 'species' ought to be. It is important to understand the difference between using the term 'species' to refer to the class of all the species in the organic world and using the term 'species' to refer to a particular group of organisms. Hull (1976, 1978) belabors this distinction. Our concern in Chapter 2 will primarily be with the former, class-oriented use of the term 'species' since we will be interested in determining whether there is a single use of the term 'species' that serves all of evolutionary biology. In Chapter 3 we will address the nature of 'species' as it refers to particular species since we will be interested in determining whether particular species are best viewed as classes with members or rather as individuals with parts.

Taxonomy in biology (traditionally called classification) has always been *hierarchical.* Within a hierarchical taxonomic scheme a lower taxonomic group is generally thought to be subsumed within the next higher taxonomic group. For example, the class 'species' has traditionally been subsumed within the class 'genera', and the class 'genera' has traditionally been subsumed within a next larger class above it, so on and so forth through various other classes finally stopping with the class 'kingdom'. Accordingly, the relationship between the higher and lower groups in a hierarchy is generally thought to be transitive. If group 1 is higher than group 2 and group 2 is higher than group 3, then group 1 is higher than group 3.[4]

In order to effectively utilize such a taxonomic hierarchy we need to be provided with definitions of the various taxa in the hierarchy. Consider possible Linnaean class definitions for the kingdoms *Plantae* and *Animalia*. Organisms within the kingdom *Plantae* can be said to be made up of cells that contain chloroplasts. Organisms within the kingdom *Animalia* can be said to be made up of cells that lack chloroplasts. Using these definitions, we can attempt to divide the organic world into two basic classes. As with *Plantae* and *Animalia*, the other taxa in a hierarchical taxonomy have a definition of

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[4] Ghiselin (1997) points out that the term 'hierarchy' has at least two different senses that need to be distinguished. An *inclusive* hierarchy is one in which higher levels do include lower levels. An example would be the relationship between undergraduate and sophomore. 'Sophomore' is included in the notion of 'undergraduate.' This is the sense of hierarchy that biological classification has traditionally used. An *incorporative* hierarchy is one in which higher levels indicate wholes of which lower levels are a part. An example might be the relationship between university, college, department, and professor. An essential feature of an incorporative hierarchy is some degree of cohesion that unifies all the parts. The levels in an inclusive hierarchy do not exhibit cohesion between them. Ghiselin notes this distinction in order to assert that traditional biological classification is best understood as an attempt to develop an incorporative hierarchy of the world's biological diversity.

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some sort associated with them. The definitions of taxa become less inclusive as one proceeds from phylum to species.

Let us consider what functions a biological *classification* has traditionally been thought to serve before considering more directly the nature of developing an acceptable species concept. Mayr and Ashlock (1991) note four traditional functions of a biological classification. First, a classification acts as a catalogue of information. More specifically, as a catalogue, a classification facilitates the efficient storage, labeling, and retrieval of information about the world's organic diversity. This is a function the Linnaean classificatory hierarchy appeared to serve quite well. Since the hierarchy only recognized roughly 300 genera and 4000 species within the kingdom *Animalia*, the everyday biologist could, with practice, retrieve information about a given organism quite readily.

The second function that Mayr and Ashlock note a classification serves is that it allows biologists to make predictions about the present and future entities in a biological class. For example, we might be able to determine the distribution of a newly discovered character in a biological class by analyzing a few well chosen organisms in the class. Mayr and Ashlock note, however, that such predictions are merely probabilistic due to the variation within classes. They suggest that a classification is judged in terms of the percentage of predictions that are confirmed.

The third function they suggest a classification serves is the development of generalizations about the entities in a biological class. Science has long put a high price on lawlike generalizations. The generalizations about higher taxa in a classification appear to withstand empirical testing rather well. For example, the following generalization about the class *Aves* appears to be lawlike: Members or parts of *Aves* have a two-legged gait. However, generalizations about various species taxa may not be as lawlike due to the variation between the entities in a species. We will address this issue more directly in Chapter 3.

Lastly, Mayr and Ashlock suggest that a classification plays a role in explaining the world's organic diversity. They suggest, however, that it is not the classification itself that does the explaining. Rather the theory *behind* the classification does the explaining. By using a particular classification scheme biologists invoke a certain explanatory scheme. For example, in light of accepting Darwin's theory of evolution a biologist will suggest that classes in a classification reflect the fact that the organisms in a particular class have descended from a common ancestor via the mechanism of natural selection. The development of a classification based on the theory of evolution, then, broadly explains why organisms with realized adaptations are grouped together.

Mayr and Ashlock's proposed functions of a classification provide us with a good starting point for getting an initial grasp on the use of a biological taxonomy, but as we will see, their proposed functions are not universally accepted. Currently there is a debate over whether the contemporary taxonomic hierarchy ought to afford biologists with generalizations. Advocates of the species-as-individuals thesis argue that species are not classes, but individuals. If species are individuals, it is hard to see how generalizations can be formulated about them. If generalizations about species are not possible, the explanatory role of the current biological taxonomic hierarchy could not follow a traditional law-like approach. Its explanatory power would need to be laid out in some other way.

Furthermore, there is a debate over whether the traditional Linnaean categories are sufficient for the purposes of modern taxonomy. Ereshefsky (1994, 1997) argues biologists ought to scrap the Linnaean categories since they are based on an outmoded theory of species. De Queiroz and Donoghue (1988) suggest biologist ought to embrace a formal distinction between *classification* and *systematization* and then aim to develop *systems* instead of *classifications*. They believe a *classification* is best seen as aiming to develop a hierarchy of classes into which organisms with similar traits are placed, whereas a *system* is best seen as aiming to develop a description of various wholes which consist of parts, namely organisms related by descent.[5] For the purposes of this dissertation we will use the terms 'taxonomy' or 'taxonomic hierarchy' to refer equally to either a classification or a systematization.

Species as Units of Evolution

Talk of taxonomy being coupled with a theory raises the question of what theory ought to underwrite our taxonomic hierarchy. Should taxonomy be connected to evolutionary theory? Consider briefly the theory behind the Linnaean classification which was widely used before Darwin's impact. The Linnaean classification was underwritten by a creationist theory of species origin. Linnaeus thought God had created

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[5] This distinction is similar to one made by Ghiselin (1997). He distinguishes between inclusive (class-oriented) hierarchies and incorporative (whole-oriented) hierarchies. See previous footnote number 3 in this chapter.

the species with essential, static properties. Hence, the Linnaean classification prior to Darwin's impact was non-evolutionary. Pre-Darwinian biologists using the Linnaean classification grouped organisms into species based on shared properties. These properties were taken to be static essential properties put in place by a higher being.

In these post-Darwinian times modern biologists no longer accept a static, creationist view of species. Instead, post-Darwinian biologists accept that taxonomy must be underwritten by evolutionary theory to some degree. One belief post-Darwinian biologists appear to share with representative pre-Darwinian biologists like Linnaeus and Aristotle is that taxonomy cannot be theory-neutral.[6] The act of classifying organisms presupposes some theory about how organisms are to be grouped. It would appear that this lack of neutrality is reflected in definitions biologists give for species (and for higher taxa as well).

Most post-Darwinian evolutionary biologists have suggested that taxonomy should reflect the actual genealogical branching process that results from evolution via the mechanism of *natural selection*. This neo-Darwinian view of biological taxonomy holds that the species taxa in our current taxonomic hierarchy reflect the least inclusive groups of organisms that have evolved and remained in relative stasis as a result of the mechanisms of natural selection and common descent; species are the *units of evolution*.

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[6] One might object to this by citing the post-Darwinian approach phenetic approach to species. We will see in Chapter 2, however, that such an approach is not viable.

Members or parts of species evolve together or stay in stasis together because they are exposed to the same biological or evolutionary forces.

Not every post-Darwinian evolutionary biologist accepts this neo-Darwinian take on the unit of evolution. Process Structuralists argue that species are the units of evolution because the organisms that make up a species are subject to various morphogenetic fields or developmental pathways.

Regardless of one's theoretical leanings, the accepted view of taxa above the species level is that they do not have biological or evolutionary forces acting upon them; higher taxa do not evolve. Hence, changes or stability within higher taxa are said to be due to changes or stability among species. The divisions used to mark higher taxa are said to be somewhat arbitrary; they merely help biologists keep track of the world's diversity and do not really reflect any natural processes.[7]

III. Summary

From a rather abstract point of view, groups of organisms are labeled as species because the groups exhibit discreteness and stability over time. With this in mind, species have two main roles within contemporary biology. On the one hand, species function as the basal taxonomic units within the current taxonomic hierarchy. On the other hand, species are identified as the units of evolution. Both of these roles are interconnected and dictate the explanatory role the term 'species' has in evolutionary biology. In order to better understand what causes discreteness and stability among groups of organisms

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[7] Ereshefsky (1991) argues against the idea that species are the only type of taxa that can evolve.

identified as species, we need to examine the various underlying causal forces that have been identified as giving rise to these groups. In Chapter 2 we will examine some of the more popular causal forces (i.e. species concepts) that have been offered by evolutionary biologists to account for discrete and stable groups of organisms.

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CHAPTER 2: THE SPECIES PROBLEM

In this chapter we will review various answers to the biological question concerning how organisms ought to be empirically identified as basal taxa species. We will call the debate surrounding this question *the species problem*. Review of this problem will ultimately provide evidence in favor of species pluralism.

As Rosenberg (1985) notes, there are various species definitions that have been advanced as a way of answering this problem. He identifies four definitions, three of which are neo-Darwinian. In this chapter we will examine seven definitions, most of which have played a significant role in the history of 20th century biology. Ereshefsky (1992) claims that there are no less than nine species concepts under serious consideration in biology. Although there is ample evidence to support his claim, some of the differences between the nine definitions he delimits are too subtle for our purposes. We will examine one theory-neutral concept (the phenetic species concept), four neo-Darwinian concepts (the biological species concept, the ecological species concept, the evolutionary species concept, and the phylogenetic species concept), and two non-Darwinian species concepts (a genetic species concept and a Structuralist species concept). For the most part, this chapter focuses on the difficulties neo-Darwinian biologists have faced in their attempts to define 'species.' We will find that these difficulties center around the wide variety of causal mechanisms that might be said to give rise to species.

We will also consider some non-Darwinian species concepts. Inclusion of these species concepts makes the species problem even more intractable, in part because consideration of non-Darwinian species concepts increases the sheer number of available species concepts, but more importantly because non-Darwinian species concepts stem from a different theoretical framework than neo-Darwinian species concepts. We will address this latter point more directly in Chapters 3 and 4. We will end this chapter by concluding that species pluralism ought to be given serious consideration in light of the wide array of causal mechanisms that can be said to give rise to species.

I. A Brief Review of Taxonomy

Before turning to consider the various species definitions, a brief review of the aims of taxonomy will be helpful. Ereshefsky (1997, 1994) claims that prior to the Darwinian revolution, the Linnaean taxonomic scheme served mainly as a helpful guide for biologists; something akin to a department store catalog. It helped them remember the characters species exhibited and the similarities between various species. In a sense, the Linnaean taxonomy had an air of neutrality about it; it lacked any explicit connection to specific theories about the organic world. Basically, it functioned as a reference guide.

The belief that the aim of biological taxonomy is to neutrally catalog the organic world is no longer widely accepted. The current view is that biological taxonomy is different from the Linnaean approach in at least two important ways. First, contemporary biologists suppose that taxonomy is integrally connected to some scientific theory. Second, they also believe that a taxonomic hierarchy carries explanatory weight. A taxonomy does not just help biologists remember, it provides or reflects an explanation for what biologists perceive.

This raises an interesting question concerning what a taxonomic hierarchy explains. Recall in Chapter 1 we noted that the motivation for delimiting species appears to be the occurrence of *discrete* clusters of organisms which exhibit *stability over time*.

Organisms throughout the organic world seem to be lumped together in various locales for long periods of time. These long lasting clusters are what biologists loosely refer to as *species*. Hence, in order to explain these long lasting clusters of organisms, biologists offer a species definition which is part of a larger taxonomic hierarchy. With this in mind, let us now examine some of the main species definitions.

II. The Phenetic Species Concept

The phenetic species concept is rooted in a theory-neutral approach to taxonomy, namely, numerical taxonomy.[1] Advocates of numerical taxonomy group organisms into taxa only according to observed similarities. They believe taxonomy should not be affected by theory, especially evolutionary theory. Hence, they aim to provide a theory-neutral taxonomy of organisms which biologists from different theoretical backgrounds can utilize. The phenetic species concept is said to be completely operational, providing a way of defining species that is based only on observable properties of organisms.

Organizing organisms according to observed similarities requires a way to measure similarity. Numerical taxonomists typically measure similarity in terms of the degree of *phenetic distance* between various organisms. The phenetic distance between organisms is measured by comparing the phenotypic differences between organisms. For example, suppose we wanted to employ the phenetic species concept to group crocodiles, lizards, and birds according to their observable similarities. Crocodiles and lizards share more observable similarities with each other than either do with birds; crocodiles and lizards are not identical but their gaits are more similar to each other's than either's are to the gait of birds, their skin is more similar to each other's than either's are to the skin of

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[1] See Sneath and Sokal (1973) for more details.

birds, etc. All things considered, these similarities put crocodiles and lizards nearer to each other on a graph which measures overall similarity than either is to birds. Hence, the phenetic distance between crocodiles and lizards is less than the phenetic distance between crocodiles and birds or lizards and birds. If the numerical taxonomist wanted to group any of the three groups together, crocodiles and lizards would be grouped together and birds would constitute their own group. Decisions about how to group organisms into species are made in a similar fashion, with the only difference being that there is less *phenetic distance* between species than there is between higher taxa. A formal definition of species might look something like the following: "a species is the set of organisms not more than *x* phenetic distance units apart."[2] Those who advocate a phenetic species concept believe that the species taxa developed by measuring phenetic distances between organisms are completely objective; the species taxon reflects real patterns in nature. Furthermore, the advocates claim the species taxa are theory neutral; one need not presuppose the truth of any theory, such as evolutionary theory, in order to develop taxa based on phenetic distance.

Numerical taxonomy has been criticized quite severely (Hull 1970, Rosenberg 1985, Sober 1993, Ridley 1996). One problem is that it cannot deliver on its promise of theory-neutrality. This problem faces the phenetic species concept at a number of different levels. For example, at a basic computational level, deciding what the appropriate value for *x* should be in the above definition turns out to be hopelessly grounded in the arbitrary decision of the biologist developing the taxonomy. Furthermore, there are numerous ways to measure phenetic distance. Should we weight

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[2] See Ridley (1996, p. 401.) for more details.

all traits the same? Should some traits be weighted more heavily than others? Either way we appear to be making either an arbitrary decision or we appear to allow theoretical preconceptions to color our development of taxa. Ultimately, the determination of traits exhibited by organisms would necessarily seem to be theoretically grounded. For example, in the event that two separate groups of researchers using the phenetic species concept develop two inconsistent sets of phenetic species, which set of species is the right one? The only apparent way to decide would be to employ various criteria of theoretical adequacy (i.e. testability, fruitfulness, scope, simplicity, etc.), to determine which set of phenetic species fairs the best. However, by employing such criteria, we admit that there is a theory underlying each set of phenetic species. Ultimately, in employing adequacy criteria to solve the problem, we wind up admitting something that the pheneticists do not want to admit.

Answering these questions about trait importance, the ordering of traits, and other questions like these lead us to the conclusion that phenetic similarity is actually a product of the biologist who is perceiving the traits. It would appear that implementation of the pheneticist position ultimately conflicts with its self-proclaimed theory-neutrality. These criticisms of the phenetic species concept prompt Rosenberg to say "there is no theory-free taxonomy and....all taxonomic decisions are about factual matters." (1985, p. 187) His point is two-fold; first, biologists must view organisms and grouping phenomena with some theory in mind, and second, future observations of the stability and diversity of groups of organisms may prompt biologists to posit new theories about how the stability and diversity of such groups are maintained. It would seem then, that all taxonomic app

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approaches, each of which offer a definition of species, are developed with some underlying theory of how groups of organisms are maintained over time in mind.

III. The Biological Species Concept

By far the most popular species concept in the 20th century has been the biological species concept. Mayr (1942, 1963) has been the most prominent advocate of the biological species concept, although Ghiselin (1974, 1987, 1989, 1997) has been a recent apologist for the concept. Mayr's version of the biological species concept is as follows, "*A species is a group of interbreeding natural populations that is reproductively isolated from other such groups.*"[3] According to advocates of the biological species concept, groups of organisms (e.g. species) are divided up by isolating mechanisms that prevent gene flow between certain organisms.[4] Although these organisms may not all fall into one population, all the populations are connected by gene flow. Each species then, represents a reproductively isolated group of organisms dispersed in one or more populations that retains its unique pool of genes. Some of the main isolating mechanisms are geographical barriers, ecological barriers, and zygote inviability. What is important here is the notion of a gene pool which stays intact over time. Gene flow among the organisms in a species contributes to the development of adaptations since such gene

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[3] Mayr and Ashlock (1991, p. 26).

[4] Following after Van Valen (1976), Ridley (1996) includes the biological species concept under the general rubric of a reproductive species concept. He does this because he points out that Paterson's recognition species concept is also biological in nature. The interbreeding species concept focuses on isolating mechanisms that impede interbreeding between organisms. The recognition species concept focuses on mechanisms that ensure interbreeding takes place. Ridley suggests these two species concepts are really just different sides of the same coin. Although one might take issue with Ridley's lumping these two together there seems to be no harm in accepting his notion of a reproductive species concept. We will, however, only focus on the biological species concept. Many

exchange ensures that only genes which interact well with other genes are selected for. Ultimately such gene flow results in the occurrence of a somewhat uniform phenotype among organisms in the gene pool. Genes that do not interact well with the rest of the genes in the pool are selected against. Advocates of the biological species concept also hold that not all the individuals need to interbreed. Some individuals may fail to interbreed. However, the important consideration is that any two individuals in a population have an equiprobability of mating and passing on genes. On the average then, a gene pool of coadapted genes is representative of all the individuals protected or preserved by the isolating mechanisms.

The classic example of the usefulness of the biological species concept is the case of closely related, yet, different mosquito species of the genus *Anopheles* located in Europe. When the outbreak of malaria occurred in Europe, it was hypothesized that malaria was transmitted by all species of *Anopheles* mosquitoes which existed all throughout Europe. However, malaria was only reported in selected areas throughout Europe. Mayr successfully showed that different species of the *Anopheles* mosquito existed even though the different species often co-existed. The difference was marked by reproductive habits. Not all of the *Anopheles* mosquitoes interbred with each other. Only organisms of two species of *Anopheles* carried the agent which caused malaria. Hence, application of the biological species concept successfully explained the outbreak of malaria in selected areas of Europe.[5]

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of the problems that plague the biological species concept also plague the recognition species concept.

[5] Paterson (1992) advocates a recognition species concept which is also biological in nature. He argues that the main cause of reproductive isolation is the inability of members of differing species to recognize species specific breeding rituals. Thus species

Problems with the Biological Species Concept

Any version of the biological species concept faces some difficulties. First off, it is not easily applied to any group phenomenon which takes place over an extended period of time. Consider the case of a series of ten generations of a species in which the organisms in the first generation are markedly different from the organisms in the tenth generation. How might we test to see if the first and tenth generations are capable of interbreeding? In most instances it is not physically possible since members of the first generation have expired by the time members of the tenth generation come into existence. We might try to invoke dispositional language and say that if members of the two generations *could* co-exist they *would be able* to interbreed. However, the use of such language does not seem to help in those cases where the phenotypic change over numerous generations is quite dramatic. Due to the possibility of mutations and polyploidy, a series of generations that are reproductively connected can potentially exhibit radical phenotypic changes between the first and tenth generation; changes so radical that members of the tenth generation could potentially develop a phenotype that does not allow them to physically reproduce with members of the first generation. In

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are groups of organisms that share a common mate recognition system. Many clear examples of such mate recognition systems can be given. For example, males of many bird species have certain dance rituals that entice females into choosing them as a mate. Also, male birds often have distinctive coloration patterns which females of the same species help us to determine conspecifics (e.g. members of the same species). Bentley and Hoy (1974) have shown that female crickets only respond to the mating songs of the males from their species. Note that it is possible for crickets or even birds of slightly different species to interbreed but such interbreeding does not occur because they do not partake in the same mate recognition systems. One problem for the recognition species concept is that it does not apply to plants and fungi.

such cases it seems we could argue that sufficiently important biological changes have occurred which warrant claiming a new species has developed by the tenth generation.

However, the advocates of the biological species concept seem resigned to recognize only one species. This is because any attempt to assess whether members of the first generation could interbreed with members of the tenth generation would rely on evidence such as phenotypic traits or genetic structures. Although such evidence might rightly be used to distinguishing between two different species in such cases, use of such evidence suggests that species might ultimately be identified via structural or morphological traits. Use of such evidence clearly falls outside the purview of the biological species concept which focuses on reproductive connections. This problem of applying the biological species concept over time need not develop in all situations where a series of reproductively connected generations exhibit change, but clearly some applications over time seem to pose problems for strict use of the biological species concept when identifying species.

In response to this temporal criticism, Mayr and Ashlock (1991) note that the biological species concept is best viewed as a *non-dimensional* concept. By *non-dimensional* they appear to mean *non-temporal*. When faced with questions about how to apply the biological species concept over time, they say the following; "The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other but the more biologically irrelevant this status becomes." (Mayr and Ashlock, 1991, p. 27). It would appear that they do not believe the species concept is of any use over extended periods of time.

Mayr and Ashlock's response to the temporal criticism seems unsatisfactory in light of biological situations like the following. Suppose we had before us at a particular moment in time a series of ten generations of giant tortoises (*Geochelone elephantopus*). This is quite possible given the long life span and annual breeding habits of mature giant tortoises. Suppose further that members of each generation primarily interbreed with members of the same generation but that there have not been any major phenotypic changes throughout the ten generations to prevent a member of the first generation from interbreeding with a member of the tenth generation. In this case it would appear that advocates of the biological species concept would suggest that the currently extant ten generations compose the species *G. elephantopus*.

However, in a case where the ten generations of a series of breeding populations are not present at the same moment in time, say in a series of ten generations of *Drosophilia melanogaster*, the organisms of which have a rather short life span, the advocates of the biological species concept would appear to plead that such a case is biologically irrelevant to the purposes of species determination. Why should the fact that some generations of *D. melanogaster* have expired make a difference? It does not seem that the expiration of generation should be biologically important, yet advocates of the biological species concept would appear to suggest that it is. The burden is on the advocates of the biological species concept to explain why we ought to treat *D. melanogaster* different from *G. elephantopus*. Without a satisfactory response to the temporal criticism, the biological species concept does not appear to address important biological circumstances involving temporally connected generations.

Another problem for the biological species concept involves the existence of groups of *asexual* organisms. Instead of being a problem concerning how to apply the biological species concept over time, this alternative problem raised by the existence of groups of asexual organisms involves a failure of the biological species concept to recognize currently extant discrete, stable groups of organisms as species. Asexual organisms do not form reproductive groups, so although asexual organisms are capable of forming discrete, stable groups over time, these groups are not recognized as species by the biological species concept.

Advocates of the biological species concept have responded to this purported problem by suggesting that groups of asexual organisms do not need to be classified as species. Ghiselin (1987) draws an analogy between groups of asexuals in biology and nonclassified entities in other scientific situations. He says, "Not every elementary particle in the universe is part of an atom. Not every part of an organism is a cell or part of one. And not every organism is part of an organization or society of a given kind." (Ghiselin 1987, p. 138) He concludes that not every organism needs to be included in a species. Hence, following Dobzhansky (1935), he calls groups of asexuals *pseudospecies*.

Ghiselin's intuition that not every organism needs to be classified within a species seems *prima facia* plausible. However, his suggestion about asexuals is difficult to swallow in light of (1) the discreteness and stability of groups of asexuals and (2) the often complex integration of groups of sexual organisms and groups of asexual organisms evolving simultaneously under the same selection pressures.[6] One example of a rather discrete and stable group of asexual organisms is bdelloid rotifers (*Bdelloidea rotifera*).[7] Bdelloid rotifers are microscopic aquatic animals that appear to have evolved via natural selection without sex. There are about 300 different species of bdelloid rotifers that are currently recognized. Other examples of discrete and stable groups of asexual organisms include blackberries (*Rubus*) and some fungi (*Penicillium*).

One might object that not all groups of asexual organisms are discrete and stable. For instance, Mayr and Ashlock (1991) note that gall wasps (*Cynipidae*) and some types of aphids (*Aphididae*) exhibit alternating intervals of asexual and sexual generations. They suggest such complex groupings of asexuals and sexuals together should not be considered species.

Although their suggestion is intuitively plausible at first glance, it seems odd in light of the following. Their suggestion would appear to require that a new species of gall wasps or aphids be named each time the generations exhibit sexual reproduction in the alternating cycles between sexual and asexual reproduction. For example, suppose the first generation of a group of gall wasps reproduced sexually. Given that this group fits the species definition for the biological species concept, this generation would constitute a species. But what happens when the next generation exhibits asexual

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[6] Mishler and Brandon (1989) go so far as to accuse Ghiselin of *voodoo* ontology for not recognizing the evolutionary importance and relatively frequent occurrence of groups of asexual organisms. See Mishler (1985) for more examples of groups of asexuals.

[7] 'bdelloid rotifer' is derived from 'Bdelloidea' which refers to the class and 'Rotifera' which refers to the phylum. The Meselson Laboratory in the Department of Molecular and Cellular Biology at Harvard University is in the process of doing a study of bdelloid rotifers. Members of the lab use ecological or morphological criteria to divide bdelloid rotifers into species. (personal conversation)

reproduction? Is each asexual gall wasp its own species since it is reproductively isolated from the others? Such a suggestion is ridiculous but it appears to be the only answer consistent with the biological species concept. Of course we could accept Ghiselin's position and say that this second generation of gall wasps is not a species. But what would we say when the third generation of gall wasps exhibits sexual reproduction again? Is the third generation of gall wasps a different species than the first generation? To make the case difficult, let us suppose there is no morphological or genetic difference between the first and third generations. Even in light of this, the advocates of the biological species concept would appear forced to say that the first and third generations are different species. This seems counterintuitive. All in all, the suggestion that asexual organisms do not form species seems a rather *ad hoc* and unsatifactory way of saving the biological species concept. The persistence of such groups of organisms and their integration with sexual organisms would appear to be good reasons for requiring a species concept to countenance asexual species.

Perhaps the most difficult challenge that the biological species concept faces is the idea that gene flow among *sexual* organisms might neither be necessary nor sufficient for species status. This idea was first discussed seriously by Erlich and Raven (1969). To show that gene flow is not necessary they cited examples of populations of cave-dwelling plants (*Pseudosinella hirsuta*) and colonies of butterflies (*Euphydryas editha*) which do not exchange genes because of geographical barriers, yet the resemblance between the populations and colonies is maintained. They argued that the various separated populations of plants and colonies of butterflies ought to both be considered species. Furthermore, they argued that the resemblance between the populations and colonies of these two species is maintained by something other than gene flow. To show that gene flow is not sufficient they cited examples of distinct groups oak tree hybrids which nonetheless exchange genes.

Stanford (1995) gives a more recent discussion of hybrid swarms and syngameons among oak trees (*Quercus*). Hybrid swarms are discrete populations formed by two parent species, the hybrid offsping of the these species, and the offspring of the backcrosses between the hybrids and the parental species. Syngameons are even more complex hybrid populations which involve a number of different species linked together as a single interbreeding unit. Stanford notes that within these hybridized groups gene flow occurs frequently, and yet within each group, significant ecological and morphological differences occur across them which may well warrant separate species labels. White oaks in California are a prime example. *Quercus garryana* is a forest tree with a deep cleft leaf feature whereas *Q. dumosa* is a shrub with a spiny leaf feature. Both are linked by persistent hybridization. Stanford further notes that we might find it important to use ecological considerations, such as similarity of resources among reproductively isolated groups, or possibly even morphological features in these hybrid populations to develop phylogenetic boundaries. However, he goes on to say:

> "If we are interested in the anatomy or physiology of organisms, whether as a principled way to draw phylogenetic divisions or a question of independent interest, it would seem to be a grave error ... to put a forest tree with deeply cleft leaves and an arid-dwelling shrub with spiny leaves in the same basket." (1995, p. 74)

These biological examples and the ones cited by Erlich and Raven suggest that interbreeding is not always a main causal factor in maintaining species. Erlich and Raven suggest that much smaller entities (i.e. single populations) are actually the units of evolution and that selection, instead of interbreeding, is the primary force that determines whether these units stay the same or evolve.[8]

In light of these criticisms, it would appear that the biological species concept fails to adequately address all biological situations that involve discrete and stable groups of organisms. We will see that this very problem plagues each and every proposed species concept. We will also find that this is the main reason why species pluralism is a rather attractive position. Let us now turn to look more closely at the ecological species concept.

IV. The Ecological Species Concept

Van Valen (1976) offers a species definition that attempts to take seriously the arguments of Erlich and Raven (1969). Van Valen's reasoning is concise; if species are mainly maintained by selective forces, then the species definition should reflect this.[9] Van Valen defines a species as follows: "A species is a lineage (or closely related set of lineages) which occupies an adaptive zone minimally different from that of any other

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[8] They also suggest that homeostatic genotypes might sometimes cause the discreteness or stability of species. A homeostatic genotype is an example of a developmental constraint. Smith *et al.* (1985) define developmental constraint as "a bias on the production of variant phenotypes or a limitation on the phenotypic variability caused by the structure, character, composition, or dynamics of the development system." A homoestatic genotype then, is a genotype that compensates for mutations by downplaying the possible effects of such mutations. Neo-Dawinians treat developmental constraints as small affects which result ultimately from adaptations and selection. However, Process Structuralists such as Webster and Goodwin (1996) attempt to make the concept of developmental constraint the center piece a comprehensive, non-Darwinian approach to taxonomy. We will examine their position more closely near the end of this chapter.

[9] We will examine the ecological and evolutionary species concept separately for two reasons; (1) although the evolutionary species concept requires species to be historically connected entities, some versions of the ecological species concept do not, and (2) the evolutionary species concept posits various lineage maintaining forces whereas the ecological species concept posits just one, i.e. selection.

lineage in its range and which evolves separately from all lineages outside its range." (1976, p. 233) Lineages can consist of clones (e.g. asexual organisms) or a series populations that share a common ancestor.[10] A population is defined as a group of organisms that interbreed more frequently with each other than with organisms outside the group. The ecological resources that a lineage exploits and the other organisms that a lineage interacts with are said to comprise the adaptive zone of that lineage. The organisms in the adaptive zone must adapt to the available resources and the environmental conditions. When organisms are produced that fall outside of the adaptive zone, they die, since they do not have the adaptations required by the adaptive zone within which they exist. Hence, selection is said to be the main causal process that maintains the discreteness and stability of the groups which occupy adaptive zones.

Ridley (1996) offers a less formal definition of the ecological species concept. According to him, the ecological species concept defines a species as a cluster or set of organisms that exploit an ecological niche or adaptive zone. Species are clusters or sets of organisms formed in response to the available ecological resources. Ridley's alternative definition of the ecological species concept implicitly raises the issue of whether or not the ecological species concept requires *historical connectedness* between the organisms that make up a species. Historically, Van Valen's definition can be seen as a modification of the evolutionary species concept (see next section) developed by Simpson (1961) which was an explicit attempt to embrace the idea that the members or parts of a species are historically connected.[11] If a species definition requires historical

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[10] Note that Van Valen's definition allows asexual organisms to be classified as species.

[11] Although, Ghiselin (1987) takes issue with Van Valen's suggestion that species are made up of sets of closely related lineages. He claims that Van Valen was trying to make

connectedness between the members or parts of a species, then a clear implication from this is that species must consist of ancestrally related lineages or a single lineage. It is important to note, however, that the ecological species concept does not need to be embrace the notion of historical connectedness; some versions embrace it, others do not.

Problems with the Ecological Species Concept

A number of problems with the ecological species concept have been raised. One problem involves identifying adaptive zones. Although adaptive zones can be identified in some biological situations, in other situations discrete adaptive zones are not apparent even though it turns out that the organisms inhabiting the area do form a discrete group. For example, Ridley (1996) suggests that in some ecological settings certain adaptation-producing resources, such as seeds, might more aptly be described as being available in a continuous range of sizes, rather than in discrete sets with gaps in between. He notes however, that various species of birds utilizing the seeds as part of the available ecological resources within these ecological settings do not form continuous traits; the bird groupings contain rather discrete traits. Ridley argues that if cases like this can be borne out for most of the adaptation-producing resources in an ecological setting, it seems likely that there is something else, besides the adaptive ecological zone, that contributes to the discreteness of the species. Most neo-Darwinian critics of the ecological species concept expressing Ridley's concern argue that the causal mechanism maintaining species in such continuous resource examples is gene flow, not selection.

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species be two different kinds of things; individuals and classes. In Chapter 3 we will discuss the difference between conceiving of species as individuals as opposed to classes.

Sober (1993) summarizes other problems for the ecological species concept. He says that on one hand there might be situations where members of a species should be considered part of different adaptive zones. More concretely, Ghiselin (1987) suggests that the various stages of development an organism finds itself in may all fall into different adaptive zones. Hence, Sober and Ghiselin claim the ecological species concept falls prey to a similar temporal problem that plagues the biological species concept.

Sober also suggests, on the other hand, that sometimes two different species might be considered part of the same adaptive zone. He offers the case of polyploid speciation as an example. Polyploid speciation occurs when parents produce an offspring that has more chomosomes than either parents which prevents the offspring from being able to interbreed with the parents or the parents' conspecifics. The fact that two discrete groups of organisms both inhabit the same adaptive zone would appear to suggest there is something other than ecological resources which maintains the discreteness over time of the two groups. Wiley (1978) furthermore suggests that when resources are plentiful, two different species can coexist in the same adaptive zone which makes the distinction between two different, uniform groups impossible on ecological grounds. Finally, Rosenberg (1985) claims the main problem for the ecological species concept is that it requires prior species discriminations to be made in order to apply the ecological species concept.

Although these criticisms pose challenging problems for advocates of the ecological species concept, a strong point in favor of the ecological species concept is the fact that ecological resources obviously have an impact on the evolution of groups of organisms, since oftentimes organisms are clearly selected for their ability to survive according to the available resources. For example, Ridley (1996) seems to suggest that an ecological species concept works well enough in cases where resource distribution is relatively discrete. In such biological situations, one might initially identify groups based on similar morphology and with further experimentation, legitimately develop an ecological basis for the perceived morphological similarities.

However, it is clear that the ecological species concept does not work well in certain biological situations. This is similar to the problem that faces the biological species concept. Neither concept adequately addresses every biological situation involving discrete and stable groups of organisms. As we will see, the acceptance of species pluralism might provide a more hospitable ground for both the biological species concept and the ecological species concept, since species pluralism would not require each concept to apply to every type of biological situation.

V. The Evolutionary Species Concept

Increasingly in the latter half of the 20th century, evolutionary biologists interested in organizing the organic world have required taxa to reflect a temporal dimension. The evolutionary species concept represents the first attempt to develop a species concept that reflects a temporal dimension. We have seen already that the biological species concept struggles a bit with defining species over an extended period of time. But even more importantly, evolutionary biologists have increasingly required that groups labeled as species mirror the actual genealogical record of the organic world. The evolutionary species concept and the phylogenetic species concept both take serious steps toward achieving these temporal and genealogical requirements.

Simpson (1961) offers the first version of the evolutionary species concept; "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary role and tendencies." (1961, p. 153) Wiley (1978) modifies Simpson's definition slightly and defines a species as "a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fates." (1978, p. 18)

Although Van Valen's ecological species concept and the evolutionary species concept both define species in terms of lineages, there is an important difference. The evolutionary species concept postulates a wide range of lineage-maintaining forces that may ultimately cause a lineage to follow a unique destiny. Ecological forces in an adaptive zone may well produce lineages, but advocates of the evolutionary species concept recognize that forces such as interbreeding and developmental or homeostatic mechanisms can also cause a lineage to have its own unique tendency and historical fate. One important characteristic that the evolutionary species concept shares with the ecological species concept is that they both allow for the inclusion of *asexual* organisms in species groupings. The fates and tendencies of asexuals does not have to be maintained by interbreeding; ecological forces or homeostatic mechanisms might also produce and maintain lineages.

Shades of Species Pluralism

In a certain sense the evolutionary species concept moves in the direction of species pluralism. The evolutionary species concept recognizes a plurality of causal processes (interbreeding, ecological, homeostatic, and others) which may cause a group of organisms to remain dicrete and stable over an extended period of time. The evolutionary species concept does impose an additional requirement that neither the biological species concept nor the ecological species concept necessarily impose. This is that species must be a *single* lineage or ancestral-descendant sequence of populations. So, although allowing a plurality of causal mechanisms, the evolutionary species concept is still monistic in the sense that (1) it requires a species to be a lineage and (2) it holds that each lineage has a unique underlying causal process (or processes) which gives rise to it. As we will see, the history-based version of the phylogenetic species concept shares these two monistic points in common with the evolutionary species concept. Although advocates of both the evolutionary and phylogenetic species concepts often talk as if there is a single, primary causal mechanism underlying each lineage that is labelled as a species, it is possible for there to be more than one causal mechanism underlying a lineage. However, none of these pluralistic aspects of the evolutionary and phylogenetic species concepts translate into a rather serious version of species pluralism since the advocates of both concepts hold that there is one correct causal account for every biological situation. We will address the nature of species pluralism more directly in Chapter 4.

Two Types of Criticisms of All Species Concepts

Criticisms of the evolutionary species concept come from many different camps. Ghiselin (1987) attacks the evolutionary species concept (and the ecological species concept) by suggesting that it will ultimately require biologists to define species according to adaptive similarities. Ghiselin believes these species identifications would be "subjective through and through." Ghiselin's criticism rings a bit hollow, however, since the biological species concept itself is faced with similar subjectivity problems. Consider trying to determine whether or not hybridization has occurred between two different species. Just how much introgression is sufficient for hybridization? This question and others like it face any advocate of the biological species concept and they are not easily answered without some degree of subjectivity creeping into the answer.

Ghiselin's criticism is important, however, because it points to two different types of criticisms evolutionary biologists might offer against a species concept.[12] On the one hand, there are criticisms which point out that the application of a species concept is unclear in the sense that it fails to produce a clear, operational method of application. It would appear that Ghiselin's criticism of the evolutionary species concept is of this methodogical type, since he claims that the correct application of this concept ultimately rests on subjective preferences of the perceiver. Also, criticisms of the phenetic species concept are of this methodological type.

On the other hand, there are criticisms which point out that a species concept fails to recognize seemingly important biological situations that it ought to recognize. It would appear that Ridley's criticism of the ecological species concept and the criticisms of the biological species concept which point out its inability to recognize both asexual groups and groups of organisms over time are of this latter type. It has been the inability

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[12] Recall that we are mainly concerned at this juncture with various *neo-Darwinian* species concepts. There are presumably other types of criticisms one might launch against non-Darwinian species concepts. For example, one might aim to show that a particular species concept is not consistent with current biological practice. As we will see in Chapter 3, Ereshefsky (1992, 1995) offers this criticism of various morphological or structural based species concepts.

on the part of the advocates of the various species concepts to adequately address the latter of these two criticisms that has prompted the move toward species pluralism.

Advocates of the phylogenetic species concept offer both types of criticisms against the evolutionary species concept. However, before we examine the phylogenetic species concept and the criticisms its advocates launch at the evolutionary species concept, it is necessary to present some more background on biological taxonomy.

VI. More Background on Biological Taxonomy[13]

The organic world consists of many diverse organisms. Taxonomy aims to organize this organic diversity. Prior to the acceptance of Darwinian theory, the recognized way of organizing organisms was by type or form. Since the world generally appears to consist of many discrete clusters of organisms that look similar, pre-Darwinian taxonomy accepted the idea that organization by appearance is the appropriate approach.[14] The Linnaean categories were used to group organisms by increasing order of similarity. With the rise of Darwin's theory of evolution, taxonomies based on mere appearances seemed problematic, since if species evolved, then they would not need to have the same appearance through time. Gradually, taxonomies began to reflect the genealogical relations between organisms, or more correctly, the genealogical relations between *groups* of organisms.

An often used description for picturing the origin of life and evolution up to the currently existing organisms and species is the notion of a *tree of life*. Early organisms

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[13] This is merely a brief sketch of biological taxonomy for the purposes of this chapter. For more detailed overviews see Mayr and Ashlock (1991, Chapters 6, 8, 9, 10), Sober (1993, Chapter 6), and Ridley (1996, Chapter 14).

[14] There are slight variations on this theme, since some advocated organizing by function but this difference is merely one of degree not kind.

and species in the history of the organic world make up the trunk of the tree and more recent organisms and species make up the tips of the tree. Under the neo-Darwinian paradigm, development of a taxonomy of the world's diversity is merely a matter of identifying the branches of the tree. Species make up the smallest branches at the top of the tree, genera incorporate groups of the species branches, families incorporate groups of the genera, and so on all the way up through the Linnaean categories.

It is important to understand that such a tree-like branching process is divergent. Branches within the tree break off from other branches but branches never reconnect with other branches; branches either continue to extend up the tree or they have future branches that split off from them. An alternative branching process is a reticulating one. In a reticulating branching process, branches often do connect up with other branches. Such a reticulate branching process is produced by the reproductive process between individual sexual organisms. For example, family genealogies represent reticulate branching processes.

With regard to the tree of life, Hennig (see Hennig 1966, figure 1) suggested that the species branches on the tree of life are made up of reticulate relations between individual organisms. Hennig supposed that the trick for those involved in taxonomy was to focus their attention at the appropriate organizational level within the hierarchy from individual organism to large groups of organisms in order to identify those groups that first begin to exhibit purely divergent branching phenomena. These groups, Hennig argued, were true species, since he believed the reticulate/divergent boundary provided a biologically-based and objective criterion for identifying species.

Those followers of Hennig's ideas formed a school of taxonomic thought which came to be known as cladism. Cladists suggest that taxonomies or *systems* must reflect the actual genealogical relations that exist in the world. *All* biological taxa, including species, are to be delimited according to actual genealogical/phylogenetic relations. According to the cladists, the way to develop a taxonomy is to follow the divergent branching process of the tree of life. What this requires is that higher taxa be *strictly monophyletic*. A group or taxon is considered to be strictly monophyletic if and only if it contains *all* and only descendants of a common ancestral species, originating from a single speciation event. Cladists impose this requirement of strict monophyly because they reject what they consider to be subjective taxonomic divisions of the reigning school of taxonomy prior to Hennig's influence; namely, evolutionary systematics which accepts a relaxed version of monophyly.

Advocates of evolutionary systematics accept a relaxed version of monophyly where a taxon (above the species level) is considered to be monophyletic if and only if it contains *only* descendants of a common ancestral species, originating from a single speciation event. It is important to note that according to this relaxed definition of monophyly, not *all* the descendants of a common ancestor need to be included in a group for that group to be considered a legitimate grouping. Over the years the various schools of taxonomy have embraced the term 'paraphyly' to refer to this relaxed version of monophyly.

Although cladists and evolutionary systematists disagree on which definition of monoplyly to use, it is important to note that both at least require that taxa be monophyletic in some sense. Both taxonomic schools hold that taxa need to reflect the actual branching process of the tree of life and they hold that deploying the concept of monophyly will ensure that all taxa reflect this process to some degree.

A further tenet of Hennig's was that taxonomists use shared *derived* characters for evidence of strictly monophyletic taxa, instead of relying on shared ancestral characters. The difference between shared derived (i.e. apomorphic) characters and shared primitive (i.e. plesiomorphic) characters is as follows. Apomorphic characters represent new characters that have evolved within a group, new in relation to the original ancestral character state. These characters are said to be shared by all members of the group. Plesiomorphic characters represent unchanged characters that a group has possessed since the original ancestral state of the characters originated. Hennig argued that apomorphic characters provide the best evidence for identifying true species, since he believed apomorphic characters provide the only objective basis for distinguishing branching events.

The main difference between the cladistic school and the evolutionary systematics school can be seen by considering how each decides to group various organisms into taxa in different biological situations. Suppose we were faced with the phylogenetic tree in Figure 1 and we wanted to group the terminal taxa first according to the cladistic approach and then according to the evolutionary systematic approach.[15] Apart from grouping them all together or considering the three taxa to constitute their own respective groups, the cladistic approach would only suggest one other possibility, grouping crocodiles and birds together and leaving lizards on its own. This is because only crocodiles and birds together constitute a monophyletic group that exhibit at least one

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[15] Figures 1 and 2 are modeled after similar figures appearing in Sober (1993).

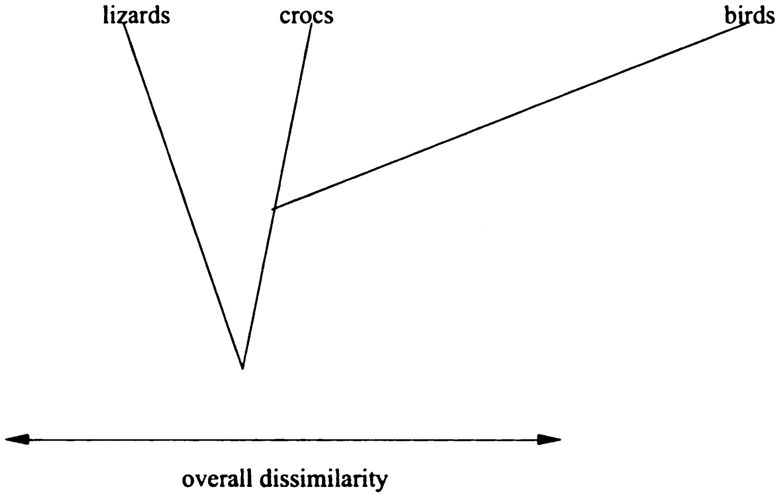

Figure 1

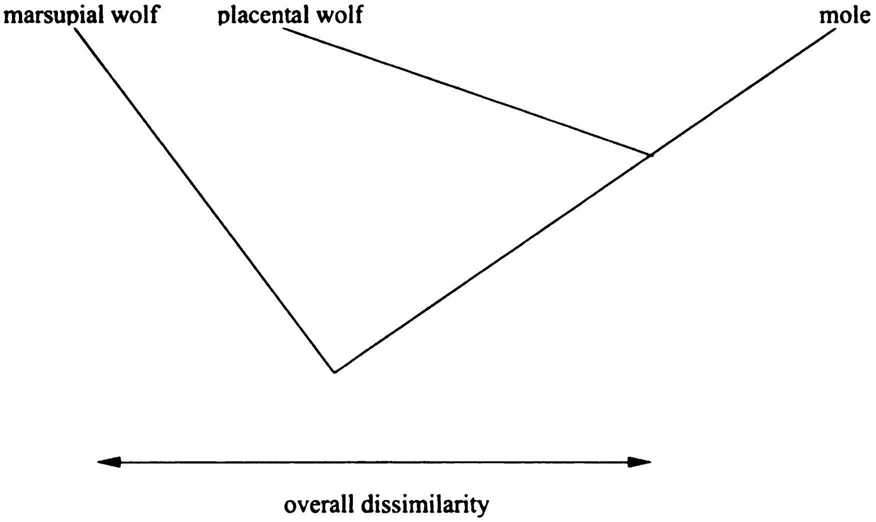

Figure 2

apomorphic character together when compared to lizards. Any other grouping of the species (e.g. birds with lizards or lizards with crocodiles) would not include *all and only* the ancestors of a common ancestral species. The evolutionary systematic approach, on the other hand (apart from grouping them all together or considering the three taxa to constitute their own respective groups), would suggest grouping crocodiles and lizards together since birds have developed unique evolutionary novelties (e.g. the adaptation for flight, two-legged gait, etc.) which distinguishes them from crocodiles and lizards.[16]

Consider being faced with the phylogenetic tree in Figure 2. In this case the cladistic and evolutionary systematic approaches would actually coincide, both would group (if they group at all) placental wolves with moles and leave marsupial wolves as its own group.[17] Notice that such groupings would be strictly monophyletic. Why does the evolutionary systematic approach follow the rule of strict monophyly in such a situation? The answer has to do with the distinction between apomorphic and plesiomorphic characters and the determination of evolutionary novelties. In the case of marsupial and placental wolves, although they both exhibit similar features, advocates of evolutionary systematics do not recognize the development of an evolutionary novelty in Figure 2. At most, it would appear that the group 'placental wolves' sustained a few character reversals which shifted the group back closer to the original ancestral state of the entire set of taxa. Without any evidence of the development of evolutionary novelties,

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[16] Note that the numerical taxonomy approach mentioned previously could also advocate grouping lizards with crocodiles but such a decision would be made merely on the grounds that lizards and crocodiles are phenetically more similar than either are to birds.

[17] Note that the numerical taxonomy approach would group marsupial and placental wolves together. Such a grouping is polyphyletic since it includes entities that do not share a common ancestor.

advocates of evolutionary systemics are inclined to group according to apomorphic characters.

Advocates of cladism always follow the evidence of apomorphic characters. This is reflected in Figures 1 and 2. Although Figure 1 shows that crocodiles and lizards share similar plesiomorphic characters (e.g. a pentadactyl limb) and that birds appear to have evolved quite separately from the crocodiles and lizards, advocates of cladism group according to the fact that birds and crocodiles share certain apomorphic characters which indicates that they appear to share a more recent common ancestor. Following Hennig, advocates of the cladistic approach argue that more recent common ancestor is more important than older ancestral characters in such instances, since recency of ancestry presumably provides a more "objective" criterion for delineating taxa.

How does all this discussion of the various approaches to classification help us understand the different species concepts? Well, the advocates of the evolutionary species concept do not require particular species to be strictly monophyletic because they want to allow for the possibility of peripatric speciation (see Mayr and Ashlock 1991, p. 89). According to this model of speciation, a small population may split off from the main species and become reproductively isolated (or become subject to different selection pressures) without geographic isolation prompting the split.[18] In such a case, the main species is said to continue on along the same evolutionary track; only the new

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[18] Allopatric speciation has traditionally been recognized as the most frequent form of speciation. Allopatric speciation occurs when a new species evolves in geographic isolation from its ancestor. Other modes of speciation have recently been suggested including parapatric speciation which occurs when a new species evolves in a population which is contiguous to other species, and sympatric speciation which occurs when a species splits into two without any separation of the ancestral species' geographic range.

peripherally isolated population has developed a new evolutionary tendency and historical fate (in otherwords, the peripherally isolated population has developed some evolutionary novelties). This example is reflected in the situation of the group 'birds' in Figure 1. Although the terminal taxa in Figure 1 are not species the idea is the same, the group 'birds' have evolved separately from the groups 'crocodiles' and 'lizards.' When the terminal taxa do actually represent more closely related groups, advocates of the evolutionary species concept (i.e. evolutionary systematists) will name paraphyletic groups as species if the evolutionary evidence warrants it.

A Purported Problem with the Evolutionary Species Concept

Advocates of the phylogenetic species concept do not allow paraphyletic groupings to be named as species because they argue the determination of paraphyletic taxa is hopelessly subjective. They believe taxonomies that deviate from the actual phylogenetic branching process are always tainted by the subjective desires of those developing the taxonomy. This is why the phylogenetic species concept focuses exclusively on genealogical relations when grouping. Thus any time a speciation event occurs, two *new* species are produced; advocates of the phylogenetic species concept hold that ancestral species do not survive branching events. They also recognize that the phylogenetic species do not represent every aspect of evolution (see Ridley 1986, p. 59) but they claim classificatory objectivity comes at such a price. We will wait to consider criticisms of the phylogenetic species concept until after it has been presented more fully. Let us now turn to the phylogenetic species concept directly.

VII. The Phylogenetic Species Concept

There have been a large number of phylogenetic species definitions offered in the recent years. Baum and Shaw (1995) divide the various phylogenetic approaches into two basic types; character-based and history-based. Although character-based phylogenetic species concepts do not reject genealogical relations as evidence for grouping species, they do not take such evidence as primary. These character-based phylogenetic species concepts are rooted in a controversial offshoot of the cladistic approach to taxonomy; namely pattern cladism or transformed cladism. We will not discuss a character-based version since such a version appears to face many of the same problems that face the phenetic species concept.[19] Instead, we will examine the more widely accepted history-based approach as offered by Brandon and Mishler (1987).[20]

Following Hennig (1966), the main aim of any history-based approach is to locate species (with regard to sexual organisms) at the point above which divergent relationships occur and below which reticulate relationships occur.[21] Doing so presumably offers taxonomists an objective criterion for identifying the least inclusive isolated groups of organisms. One way to attempt this is by using monophyly in conjunction with a *ranking* criterion which identifies an underlying causal force.

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[19] See Cracraft (1983, 1989), Ereshefsky (1989), Nixon and Wheeler (1990), (Davis and Nixon 1992), Baum and Donoghue (1995), and Baum and Shaw (1995) for discussion and criticism of the character-based approach.

[20] Ridley (1989) offers a version that is comparable to Mishler and Brandon. Furthermore, Baum and Donoghue (1995), Baum and Shaw (1995), and Graybeal (1995) all offer versions of a history-based phylogenetic species concept based on gene coalescent theory.

[21] Asexuals will need to be treated differently since each reproductive act of an asexual organism constitutes the start of a new lineage. This point will be raised shortly as a criticism of Mishler and Brandon's approach.

Advocates of the history-based phylogenetic species concept must rely on some underlying causal force when identifying species, otherwise one would not be able to distinguish species.[22] Thus, species are "ranked" or identified according to the causal mechanism (or mechanisms) which gives rise to the various discrete and stable groups of organisms.

Recall that strict monophyly is a concept that was introduced by the cladistic school of classification in order to facilitate the identification of taxa according to the phylogenetic branching process of the tree of life. Although monophyly was originally defined using species as part of the definition, advocates of the phylogenetic species concept suggest redefining monophyly so that it *applies* to species and not just higher taxa. Mishler and Brandon (1987) offer a version that incorporates a redefined conception of monophyly.[23]

Mishler and Brandon (1987)

Mishler and Brandon offer a definition of species that stems from a phylogenetic point of view. They note that various answers to the neo-Darwinian species problem have been proposed, and they point out that none of these answers is applicable to every

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[22] Ereshefsky (1989) criticizes the phylogenetic species concept on the grounds that it fails to identify species based on causal mechanisms in the way that other species concepts do. However, Mishler and Brandon (1987) appear to have this problem solved.

[23] Another way to attempt to locate species at the boundary of divergent and reticulate relationships is to utilize a related concept to monophyly, that of exclusivity. Baum and Shaw (1995), Baum and Donoghue (1995), and Graybeal (1995) all offer history-based approaches that utilize exclusivity when locating species. Exclusivity aims at identifying both reticulate groups that contain more closely related members than other possible groupings as species *as well as* divergent groups that contain all and only descendants of a common ancestor as species. Discussion of the approach offered by Mishler and Brandon will be sufficient for understanding the basic motivation of the history-based phylogenetic species concept.

biological situation. As a result, they believe taking a phylogenetic approach to defining species will solve the neo-Darwinian species problem. They define their phylogenetic species concept as follows:

> "A species is the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly (usually, but not always restricted to the presence of synapomorphies), that is ranked as a species because it is the smallest "important" lineage deemed worthy of formal recognition, where "important" refers to the action of those processes that are dominant in producing and maintaining lineages in a particular case." (Reprinted in Brandon (1996), p. 115)

Evidence of strictly monophyletic taxa is often provided by the identification of apomorphic characters (i.e. synapomorphies) within each group.

Mishler and Brandon recognize that monophyly needs to be redefined, because it is typically a concept that applies above the species level, so they offer the following revamped version of monophyly:

> "A monophyletic taxon is a group that contains all and only descendants of a common ancestor, originating in a single event." (Reprinted in Brandon (1996), p. 118)

Their revamped version of monophyly does not require that a specific causal process be identified as the originating event of a taxon. They suggest that the originating "event" of a taxon could simply be a single individual, a kin group, or even a population. However, this newly defined concept of monophyly still requires two new species to be named when a new branch splits off from an existing one.

Shades of Pluralism Again

Mishler and Brandon suggest their phylogenetic species concept is monistic with respect to what counts as a *group* (or taxon). All species taxa must meet the criterion of strict monophyly, since, as argued by Hennig (1966), this ensures that species taxa accurately reflect the actual branching process of the tree of life. However, Mishler and Brandon recognize that the concept of strict monophyly is insufficient for determining which chunks of the phylogenetic tree are to be considered species. In light of this recognition, they suggest that various causal processes such as interbreeding, homeostatic mechanisms, and selection can act as *ranking* or identifying criteria for picking out which monophyletic groups that exhibit shared derived characters are to be considered species taxa.[24] Hence, they suggest their version of the phylogenetic species concept is *pluralistic* because it allows the use of different causal criteria when determining what chunks (i.e lineages) of the phylogenetic tree of life should be identified (or as they say "ranked") as species.

Their version of pluralism is somewhat limited since they suggest that no more than one ranking (i.e. identifying) criterion may be used to pick out any given chunk of the phylogenetic tree of life. Importantly, their version does allow deployment of a different ranking criterion if one moves to consider a different chunk in the tree of life. For example, in one biological situation a group of organisms may be ranked (i.e. identified) as a species because they form an interbreeding group, whereas in a separate biological situation the organisms involved may be ranked (i.e. identified) as a species because they experience the same selective pressures. However, in neither situation can both ranking (i.e. identifying) criteria be deployed. The bottom line is that there is one unique tree of life; some parts of it are called species because of the process of interbreeding whereas other parts of it are called species because of the process of

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[24] Mishler and Brandon do not actually give explicit examples of biological processes other than that of interbreeding, although from their comments about asexuals forming

selection and still other parts are called species because of some other causal process.[25] Although somewhat pluralistic, their version is not a serious version of species pluralism since it endorses the idea that there is one correct causal story for each part of the tree of life.

Mishler and Brandon advocate using apomorphic characters to help pick out species; however, such characters are merely used as *evidence* for historical relations. The idea is that the existence of apomorphic characters between organisms within a discrete, stable group provides sufficient grounds for inferring the existence of a lineage being maintained by some underlying causal process.[26] This use of apomorphic characters to help determine species offers Mishler and Brandon two main advantages over other phylogenetic species concepts that are primarily character-based. First, the use of such characters provides a somewhat operational method for determining species. As noted earlier, interbreeding is often difficult to test, especially over time. This same

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discrete and stable groups in a way that does not involve interbreeding, they seem to imply that selective forces can be used to pick out such groups.

[25] It should be noted that Ridley (1989) offers a version of a history-based phylogenetic species concept which he calls the cladistic species concept. Ridley defines a species as *"that set of organisms between two speciation events, or between one speciation event and one extinction event, or that are descended from a speciation event*." Although he uses the word 'set,' this is merely a way of speaking since, like Mishler and Brandon, Ridley suggests that species should be monophyletic. Each species is monophyletic up to the end of their existence, that is, it includes all the ancestors from the point of a speciation event up until another speciation event occurs or the species goes extinct. Ridley notes that the cladistic species concept needs to give an account of speciation or splitting and he suggests that joint use of the biological species concept and the ecological species concept can do this. As we will see, Ridley criticizes some aspects of Mishler and Brandon's account. His criticisms will provide a basis for calling the history-based phylogenetic species concept into question.

[26] Although different, Mishler and Brandon's use of apomorphic characters is connected to the cladistic school's adherence to parsimony as a principle for inferring phylogenies. See Sober (1988) for a detailed discussion.

problem arises for other biological processes as well. Mishler and Brandon argue the use of apomorphic characters eases this problem slightly by providing a purportedly objective basis for testing inferred branching events. Second, Mishler and Brandon argue their approach avoids the problem of recognizing too many discontinuities which plagues a phylogenetic species concept based primarily on characters, since their history-based phylogenetic concept links apomorphic characters to a biological process that acts upon lineages. This insures that multitudes of small discontinuities (e.g. fixed characters exhibited by just a few individual organisms) do not end up providing a basis for a species taxon.[27]

Minor Problems with the Phylogenetic Species Concept

Mishler and Brandon mention that species united by reproductive forces are sometimes difficult to pick out because species do not always exhibit discrete reproductive boundaries. Interbreeding sometimes conflicts with the evidence of apomorphic characters. For example, interbreeding groups often appear to exist which include members from a number of lineages that each exhibit their own apomorphic characters. Since there is evidence of apomorphic characters, such an interbreeding group could not yet be named a single species. However, Mishler and Brandon suggest the appearance of separate lineages might merely be the result of limited epistemic access. A larger lineage might be in the process of forming. It may currently only appear

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[27] Ridley (1989) criticizes Mishler and Brandon's use of apomorphic characters to help pick out species. However, by rejecting the use of any characters whatsoever, it appears that the account offered by Ridley is faced with an insurmountable operational difficulty. Theoretically, his cladistic species concept seems to fit well with the evolutionary process of divergence. However, by failing to provide a definition that is testable to any significant degree it seems that his definition is of little practical use.

as if a number of different lineages have members that interbreed. Given more time the different lineages would no longer appear to be separate but merely different aspects of one larger lineage. Mishler and Brandon suggest the answer to this operational problem is to label such unresolved lineages *metaspecies* on the assumption that since the groups are exchanging genes, gene flow will act to unify the small lineages into a larger one.

Sober (1993) argues that using monophyly to identify species does not work as Mishler and Brandon intended, since whenever a new branching event occurs, the new species by definition do not contain any of the ancestors of the previously existing species. (Recall that the cladistic school supposes that ancestral lineages do not survive branching events.) Hence, Sober rightly points out that phylogenetic species, as recognized by Mishler and Brandon are not truly monophyletic. However, Sober's criticism is easily subverted by tweaking the definition of monophyly to reflect the break points between lineages. For example, Ridley (1989) solves this problem by stipulating that species be recognized as monophyletic groupings *between lineage branching events*. Of course, employing this tweaked definition when identifying species still requires that branching events be identifiable. This is why Mishler and Brandon advocate the use of "ranking" criteria which refer to some underlying causal mechanism in their phylogenetic species concept.

Before considering somewhat more fundamental problems with Mishler and Brandon's approach, it is worth noting one specific benefit their version of the phylogenetic species concept offers that many other versions do not; *their version allows asexual organisms to be grouped as species*. They suggest that through continued reproduction of offspring, asexual organisms can be said to form monophyletic lineages.

Furthermore, the pluralistic aspect of their phylogenetic species concept does not require lineages to meet the criterion of interbreeding; other processes can maintain the stability and discreteness apparent in asexual lineages, such as uniform selective forces or homeostatic mechanisms.

Ridley (1989), although advocating a similar version of a history-based phylogenetic species concept, is not convinced that a plurality of causal ranking criteria is necessary. He argues Mishler and Brandon have not given clear examples where interbreeding fails to pick out species lineages. He claims their best example; groups of asexual organisms, admits of varying interpretations regarding whether they are held in place by selective pressures due to ecological resources. The example of bdelloid rotifers, however, is again instructive. Mishler and Brandon (1987) cite a data from a colleague (Holman) which shows that systematists recognize asexual rotifers more consistently than their sexual counterparts, monogont rotifers. If this is true, it seems that groups of asexuals may exhibit discreteness and stability that is worthy of classificatory status; discreteness and stability that is by definition not due to interbreeding. Furthermore, in his criticisms Ridley seems to unfairly assume that the only other option available, besides the interbreeding criterion, is selective pressure. Mishler (1985) has shown that *developmental criteria* (e.g. homeostatic mechanisms) can successfully be used to pick out species of asexual bryophytes.

Major Problems with the Phylogenetic Species Concept

Mishler and Brandon's phylogenetic species concept also faces some rather difficult problems. One such problem is that it is not clear that metaspecies will always converge into a single lineage. Recall the evidence offered by Erlich and Raven (1969) which supports the claim that gene flow is not always sufficient for maintaining unity among organisms. Stanford (1995) summarizes the example of oak hybridization to illustrate this very point. It seems, therefore, that interbreeding between separate lineages exhibiting their own unique characters can occur without these lineages converging into one single lineage at some time in the future. Mishler and Brandon might reply that in such cases, selective pressures of the ecological setting might provide the underlying causal mechanism necessary to name the lineages different species. Although this is a plausible response, it is interesting that Mishler and Brandon do not offer it.

Furthermore, it isn't clear which response is preferable. How should one decide between whether to name a single metaspecies or name a number of species based on selective pressures? Although the original problem posed by metaspecies may ultimately be answerable, answering the metaspecies problem does appear to raise some operational problems. Mishler and Brandon's species concept does not appear to provide biologists with a completely clear method for determining species. In difficult cases such as the metaspecies case, it would appear that species determinations are a bit uninformed and rather arbitrary. Although such uninformedness and arbitrariness may eventually be resolved as time proceeds, as we will see, the problem of uninformed and arbitrary decisions infecting species determinations is a bigger problem than most advocates of the phylogenetic species concept want to admit.

The evidence discussed by Stanford (1995) concerning hybridization raises another difficult problem for the phylogenetic species concept. Cases where hybridization occurs between lineages results in a phylogeny that exhibits reticulate branching. This would seem to pose a problem for Mishler and Brandon's strict monophyly criterion. In response, they suggest that hybrids are merely short lived and only appear to pose a problem because we lack sufficient foresight into the future when the reticulate branching disappears. Hence, they suggest hybrids need not be recognized as species. This reply is problematic for at least two reasons. First, not all hybrids are short-lived, the oaks example seems a case in point. Hence, the problem with hybrids producing reticulate branching processes will not just go away when the future is revealed. Second, their reply seems reminiscent of Ghiselin's *ad hoc* insistence that apparently stable groups of asexual organisms need not be identified as species. Not including significant biological phenomena into a classification scheme because it fails to fit a circumscribed definition of monophyly seems unwarranted given the frequency of hybridization in the organic world.

Although he endorses a phylogenetic approach, Ridley (1989) notes two major objections which confront any version of the history-based phylogenetic species concept. First, such a concept necessarily denies the survival of species through splitting events, and second, the concept necessarily denies the existence of anagenetic speciation. The first problem arises if one takes notice of the evolutionary rates of various lineages within a phylogenetic tree. Evolutionary systematists argue that certain lineages evolve novelties and branch away from and evolve more quickly or slowly than the parent lineage. When such a branching occurs, the naming of a separate paraphyletic taxon that evolves at a rate different rate from the original lineage might well be warranted. The existence of adaptive gaps in the environment and the peripheral isolation of a population from the main species population each allow for rapid evolutionary changes to occur in a lineage. Advocates of the evolutionary species concept claim such evolutionary differentiation is important enough to warrant classificatory status.

In response, Ridley (1989, 1996) claims that the desire to name paraphyletic taxa as species is ultimately grounded in phenetic considerations which are hopelessly arbitrary. As a result he rejects such taxa. This response has the appearance of attacking a strawman. Ereshefsky (1991) and Sober (1988) both persuasively argue that boundaries in biology are fuzzy instead of sharp. It is undeniable that evolutionary divergence occurs. Although it is difficult to give necessary and sufficient conditions for when enough divergence in a lineage has occurred to warrant naming a paraphyletic taxon, there are certainly clear cases where sufficient divergence has occurred. The divergence of the taxon *Aves* from the paraphyletic taxon *Reptilia* seems a clear example. Also, the use of paleontological data might provide some evidence for saying that sufficient divergence has occurred.

It is important to note that the determination of evolutionary divergence really does not rest on any less secure *epistemic* grounds than the determination of actual genealogical relations as required by the phylogenetic species concept. Recall that the phylogenetic species concept is rooted in the cladistic school of taxonomy which argues that the actual genealogical relations provide an "objective" basis for a taxonomy. Advocates of the school claim that such relations actually exist in the world, so the relations provide an objective basis for picking out taxa, including species.[28] Such a

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[28] Michael Ridley has been a staunch defender of such a position. See Ridley (1986, 1989, 1990, 1996).

claim appears reasonable, yet it seems that the advocates of the phylogenetic species concept may hide how difficult the determination of such relations actually is.

There would appear to be epistemic difficulties facing *any* species concept that relies on determining the relationships between various organisms. Any attempt at reconstructing the *actual* phylogenetic record will often fail to bridge the gap between what biologists hypothesize the record to be and what the record actually is. The associated biological processes are often too complex and intricate to provide biologists with knowledge of the *actual* relations that has a high degree of certainty attached to it.

Consider some specific methodological decisions facing advocates of the phylogenetic species concept.[29] First, they need to commit to a theory about the nature of character states and their allowable changes. What type of characters ought be used as evidence for changes in a lineage, discrete or continuous? Eye color and type of gait are examples of discrete characters, whereas beak size and body length are examples of continuous characters. If discrete ones are used, how many states are there for each character? If continuous characters are used, where does one draw the line between the various states? Can there be character reversals? A reversal involves a change to a transformed state and then back again to the original state. Can reversals occur more than once? If there are more than three character states, how are they to be ordered? Any species concept that requires answers to these questions would seem invariably colored *by the views of the investigator* who is presupposing (1) a certain model of evolution and (2) a theory about characters. This coloration would appear to make the exact

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[29] Maddison and Maddison (1992) give a much larger overview of the types of decisions that need to be made when inferring a phylogeny. What appears here is a brief synopsis.

determination of actual phylogenetic record difficult. This difficulty can be seen when the answers to the above questions are changed; a different account of the phylogenetic record is obtained by those using different models of evolution and different theories about characters.

Other methodological commitments by advocates of the phylogenetic species concept need to be made as well. Regarding derived and ancestral characters, how is one to tell which character is derived and which is ancestral? The popular answer is to determine character *polarity* (i.e. the direction of character flow) by comparing the characters under consideration to the characters of an external taxon. This however, is not always conclusive and is not always an option, since an external taxon is not always identifiable. Furthermore, another difficult problem involves how one ought to compile the characters when inferring the actual phylogeny. Should one use parsimony or maximum likelihood or some other method to organize the characters into a representative tree?[30] One might claim that the development of a consensus tree using all the various methods is the answer to this problem. However, a consensus method does not insure that the actual tree of life is identified, since consensus can be done in different ways and the resulting representations of the tree of life often differs in each case.[31]

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[30] Briefly, the method of parsimony suggests that the correct tree is the one that has the least amount of character changes. The idea is that evolution of a character more than once is unlikely, hence the tree most likely to reflect the actual phylogeny is the one with the least amount of character changes. Maximum likelihood, on the other hand, suggests that some types of character changes are more likely to occur numerous times than others, hence the tree that best reflects the actual phylogeny will be the one that takes these likelihoods into account. See Sober (1988) for more details.

[31] See Barrett, Donoghue, and Sober (1991).

Should the history-based phylogenetic species concept be rejected as a result of these methodological/epstimological problems? Absolutely not. Certainly biologists advocating a certain methodology can devise experiments and try to test which relations make up the actual phylogenetic record. The problem with testing evolutionary relations, however, is that evolution is difficult to test. Testing an evolutionary hypothesis requires many, many years.

The upshot of this discussion, recalling Rosenberg (1985), is that *any* attempt to define species needs to make certain theoretical commitments regarding how biological phenomena are to be interpreted. This is not bad, but it requires that evolutionary biologists temper their claims regarding how well their findings represent the actual world. Although the history-based phylogenetic species concept *attempts* to get at the actual phylogenetic record, this is not conclusive evidence in its favor. The methods used by advocates of the phylogenetic species concept are no more foolproof than the methods used by advocates of other species concepts. Advocates of other species concepts aim to group species according to other *actual* biological processes. The phylogenetic species concept does not have the market cornered on the attempt to identify real facts about the biological world. In light of this discussion, it would appear that the naming of paraphyletic taxa by advocates of the evolutionary species concept is no more problematic than the determination of strictly monophyletic taxa.[32]

Kitcher's (*) Principle

Some evolutionary systematists criticize the phylogenetic species concept because it denies anagenetic speciation. Ridley (1989) claims that such opposition is merely

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[32] Mayr and Ashlock (1991) hold this same position throughout Chapter 9 of their text.

grounded in phenetic considerations. However, in an attempt to show the limited focus of the the cladistic school (which favors a phylogenetic species concept), Kitcher (1989) offers some puzzles which he believes face any attempt to identify species strictly according to lineage splittings.

To generate sympathy for these puzzles he offers something called the (*) principle. Basically the (*) principle holds that a proposal to call the parts of a lineage a species should only depend on the properties and relations *intrinsic to the parts in the lineage in question* and not on the properties and relations of parts of other lineages (future, concurrent, or past). With this principle in mind, let us consider the first of two puzzles offered by Kitcher (1989).

Suppose there are two worlds, W_1 and W_2. In W_1 there is a lineage that undergoes a speciation event at time t_n that divides it into two different lineages. Call the part of the lineage before t_n stage A and the two separate lineages after t_n parts B and C respectively. Further suppose that after a hundred years (time t_{n+100}), a catastrophe occurs which wipes out part C. Eventhough part C is wiped out after a hundred years, advocates of the history-based phylogenetic species concept would identify three different species, each corresponding to the three parts A, B, and C. In world W_2, suppose everything is the same except that the catastrophe which wipes out part C happens immediately after time t_n, (call it time $t_{n+0.00000001}$). Further suppose that the ancestral lineage (part A prior to t_n) in both worlds follows the same evolutionary fate and tendency when it becomes part B after the split at time t_n. Kitcher argues that since advocates of the phylogenetic species concept would hold that speciation would be said to have occurred in W_1, speciation within the ancestral lineage in W_2 should be said to have occurred as well. This follows from acceptance of the (*) principle which holds that the fates of the organisms destroyed by catastrophes in both worlds are irrelevant to the identity of the organisms in the lineage identified in part B. Kitcher believes this puzzle (and others) are evidence in favor of the conclusion that biologists should countenance anagenetic speciation. [33]

Kitcher's puzzle strikes against the hegemonic use of splitting as the necessary indicator of groups worthy of taxonomic status. The point of Kitcher's puzzle is that it is possible for *the same causal process*, e.g. the same bottlenecking effect, to occur in two separate cases of anagenesis and cladogenesis, yet advocates of the phylogenetic species concept maintain that only the cladogenetic case is said to involve speciation. Why? The reason seems to be because there is empirical *evidence*, in the form of two separate groups, that two branches survived the bottlenecking in the cladogenetic case. Kitcher claims such a species determination is rather whimsical since the same causal process occurs in world W_2 as in W_1. Although advocates of the phylogenetic species concept hold that the proximity of the catastrophe to the lineage split in W_2 is relevant to speciation determination, Kitcher's point is that it is the *process* that is important, not the catastrophe. Kitcher suggests we ought to accept the (*) principle and develop some way of recognizing anagenesis as a form of speciation giving that relevant causal processes can be identified apart from the evidence provided by branch splitting.

Should we accept Kitcher's (*) principle?[34] There appear to be good reasons for doing so. Failure to accept the (*) principle may undermine scientific goals such as

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[33] Dennett (1995, p. 295-96) offers a variation of this possible world situation.

[34] Stanford (1995) claims that Kitcher's (*) principle can be explained away by the fact that species are unreal. However, he uses an odd sense of the term *unreal* to substantiate this claim. He argues that since species definitions repeatedly change with theoretical contexts, species are therefore unreal. He seems to unjustifiably hold that *theory-*

completeness or comprehensiveness. For example, rejecting the (*) principle would apparently force us to embrace the notion that biologists do not name all uniquely stable or discrete groups of organisms as species *even though the groups that are not included potentially have the same causal basis as those groups that are named as species*. Although, as suggested earlier, all biological inquiry appears resigned to be colored by theoretical commitments when determining species groups, the rejection of the (*) principle seems unexplicable in light of a serious commitment to producing a comprehensive or complete scientific theory. The motivation behind the rejection of the (*) principle by advocates of the phylogenetic species concept reflects a commitment to a particular theoretical approach that not all biologists share.

Of course advocates of a history-based phylogenetic species concept might object that anagenesis is just too difficult to detect. In response to this, one avenue to explore when searching for evidence of anagenesis might be to use the biological species concept or the ecological species concept to divide up a single, non-branching lineage into two or more stable or discrete groups. It seems plausible to suggest that one might use the biological species concept to divide a single lineage whose extremes are unable to interbreed into two groups. Use of the ecological species concept might provide a similar method for dividing up a single lineage. Furthermore, we might utilize multiple species concepts simultaneously to divide up a single, non-branching lineage. Lastly, it seems that we might rely on paleontogical data from apparent failed branching attempts to help determine when significant shifts in a single lineage might have occurred.

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dependence indicates *unreality*. It seems more plausible to suggest species are real and to just accept the (*) principle.

In principle, using various species concepts (individually or jointly) to identify discrete and stable groups of a non-branching lineage is no different than using the same concepts to identify discrete and stable groups after a branching event has occurred. However, the use of these concepts to identify groups in a single lineage may not be very precise. A possible response to this objection is that *biological phenomena are imprecise*.[35] Just as we know when to say someone is bald without having a precise notion of where to draw the line between bald and non-bald, we can plausibly know when the extreme ends of a lineage cannot interbreed or inhabit different ecological niches without being able to pinpoint exactly when the inability to interbreed or the switch to a different niche occurred along the lineage.

Summary of the Species Problem from a neo-Darwinian Perspective

In light of the criticisms of the history-based phylogenetic species concept and the various criticisms of the other species concepts, it would appear that contemporary evolutionary biology is faced with a problem. No single species concept seems uniquely able to address every biologically interesting grouping phenomena. Although we might rule out some species concepts such as the phenetic species concept or the character-based phylogenetic species concept on the grounds that they face many insurmountable theoretical problems, we are still left with a number of alternatives to choose from. Although the various species concepts all seem to offer important benefits to taxonomy and evolutionary biology, each species concept appears unable to meet the various demands and interests of biologists. In spite of the troubles faced by accepting a single species concept, species monism has a strong hold on many biologists. Even while

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[35] See Ereshefsky (1991) and Sober (1980) for support of this position.

accepting species monism, some biologists openly admit that the species concept they have chosen does not identify every stable and discrete group of organisms as a species.[36] Others attempt to downplay the differences between the various concepts by suggesting they are all practical applications of a single underlying theoretical concept that has yet to be precisely identified.[37] The aim of the discussion throughout this chapter so far has been to show that neither of these attempts at saving monism is ultimately satisfactory. As we have seen, there are a wide variety of biologically important events that appear to warrant identification of species. Furthermore, sticking with one species concept will fail to address every biological event. In light of this trouble with species monism, some have advocated a pluralistic approach to defining species.[38] Basically, species pluralism is the view that there is no single correct species concept that can address every biological situation. Advocates of species pluralism argue that in light of the troubles facing the attempt at identifying a single species concept, a pluralistic approach to species is necessary.

VIII. Other Species Concepts?

We will explore species pluralism in more detail in Chapter 4. As we will see, one of the problems facing any version of species pluralism concerns the types of species concepts that biologists ought to employ. Of particular concern is whether non-Darwinian species concepts ought to be considered legitimate. This is a concern since non-Darwinian species concepts potentially produce polyphyletic taxa, (i.e. taxa that

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[36] Hull (1987), Ghiselin (1987), Mayr (1987, 1989).

[37] Ridley (1986, 1989, 1990, 1996) represents this approach.

[38] Kitcher (1984a, 1984b), Ereshefsky (1992), Dupré (1993) and Stanford (1995) represent this approach.

include organisms that have descended from more than one ancestor). Recall that the central problem of this dissertation is how advocates of species pluralism ought to structure species pluralism so as to include the maximum number of biological interests without giving way to theoretical unmanageability. We will now examine some serious examples of non-Darwinian species concepts in anticipation of this central problem facing advocates of species pluralism.

A Genetic Species Concept

Caplan (1980, 1981) and Kitts and Kitts (1979) have argued that species can be defined via some underlying genetic cause. Although such a view is not widely embraced by evolutionary biologists, brief consideration of this approach to defining species will help underscore some contemporary claims about species concepts and also begin to lay a foundation for consideration of the problems facing species pluralism. Caplan (1980) notes that species taxa are usually grouped according to traits. However, he also notes that taxonomists are also concerned with causes of similar traits. Caplan holds that similar traits result from similar causes, and these causes are either genetic or environmental. He goes on to claim that it should be no surprise that there are similar underlying causes to the similar traits we observe. However, what makes the elucidation of the underlying causes difficult is the fact that phenotypes are the only measure we have of the underlying causes and the resolving power of such a measure is rather poor. Hence, each species has a unique genotype but we do not, as of yet, have access to these genotypes.

Caplan (1981) notes that genes change and mutate which may lead some to claim that organisms within a species do not necessarily have common properties. He responds by suggesting a list of genotype grouping criteria; "commonality in structure, location, function, coded messages, or modes of transcription and gene action." He also mentions 'sex' chromosomes and 'lethal' genes as possible bases for classification. He claims, "All that the structural variability of the gene shows is that more than one class or kind of gene or genotype may exist over time. It does not show that distinctive and common attributes of genotypes have not and cannot exist." (1981, pp. 133-34)[39]

Hull (1981) criticizes this genetic approach to species on the grounds that it offers the wrong type of explanation for the discrete and stable clusters of organisms we see. Hull attacks Caplan by suggesting he relies on the pheneticist approach to classification. He characterizes the difference between Caplan and himself as follows;

> "I place much greater emphasis on interbreeding than Caplan does. To Caplan it is just indicative of something else--genotypic similarity. To me it is fundamental in its own right. To Caplan, two organisms can be interbred because they are genotypically similar. To me, two organisms produce genetically similar organisms because they interbreed." (1981, p. 145)

Hull's criticism underscores the neo-Darwinian belief that a species concept must refer to some underlying *evolutionary* mechanism which maintains the species group. Insofar as Caplan's species concept fails to give a causal account of genotypic similarity, neo-Darwinians such as Hull, see it as incomplete.

A Structuralist Species Concept

Not every non-Darwinian approach to species is this incomplete. Process Structuralists offer a rather comprehensive approach to organizing the world's organic

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[39] Kitts and Kitts (1979) hold a similar position. They claim that species are practically identified as reproductively isolated groups of interbreeding organisms but they claim that the genetic structure of an organism explains its reproductive isolation or

diversity which is distinctly developmental in nature. This approach offers a more serious challenge to neo-Darwinism. [40]

The modern synthesis has given rise to neo-Darwinism which has explained many long-standing problems of evolutionary theory. Neo-Darwinians hold that the theory of natural selection is central to all of biology. Embryology and developmental biology have been overlooked in light of the emphasis on neo-Darwinism. Process Structuralists believe that current biology emphasizes potential to change at the expense of contraints on change.

Developmental biology has been largely ignored by neo-Darwinians, mostly because identifying the causal account of the development of the organism from genotype to phenotype is viewed as irrelevant for the purposes of selection. Most biologists interested in developmental processes merely call for methodological revisions in the current neo-Darwinian research programme. Some of these revisions include relaxing the atomistic view of traits (i.e. believing that traits are discrete and straightforwardly controlled by a small set of genes) and furthermore relaxing the belief that genic effects are deterministic (i.e. assuming that if one has knowledge of the genes, then one has knowledge of the ontogeny). Process Structuralists call for more sweeping revisions within evolutionary biology. They suggest something akin to a Kuhnian revolution in

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interbreeding capability with other organisms. They admit, however, that they do not know what the genetic structure of the various species are.

[40] It is worth noting that Ridley (1996) offers a brief synopsis of a similar taxonomic approach which he calls adaptive classification. Such an approach attempts to group organisms into basal taxa according to the adaptations they possess. Basal adaptive taxa are similar to the structural species discussed here in the sense that genealogy is not a factor for delineating either types of taxa. However, adaptative taxa would appear to have a neo-Darwinian basis unlike the structuralist counterpart discussed here.

which the Process Structuralist paradigm replaces the neo-Darwinian paradigm. Following the pre-Darwinian rational morphologists, Process Structuralists believe "that an understanding of the ontogenetic process is essential to any explanation of adult form." (Smith 1992, p. 433) Process Structuralists attempt to revive this old biological trend in the hopes of finding a more "rational" ground for understanding organic form than the current neo-Darwinian paradigm.

Process Structuralists advance the idea that evolutionary changes can be explained by identifying the series of available underlying morphogenetic processes or transformations which dictate the forms exhibited by various species members. The basic idea is that there is a limited number of pathways a newly conceived organism of a given species can follow. Process Structuralists call these pathways *morphogenetic or transformational fields*. These fields contain various collections of developmental processes such as molecular synthesis, gene activations, spatial patterning of substances, cell interactions, and morphogenetic movements. The fields then, are a collection of forces that impinge upon the development of organisms. Evolution occurs when these fields shift in subtle ways that end up affecting the development of organisms. Process Structuralists aim to develop general laws about the various morphogenetic or transformational fields that are said to govern the development of organisms.

The groups of organisms recognized as species taxa are viewed by Process Structuralists as groups of organisms which share a common morphogenetic or transformational field. Genealogical relations are not believed to be a primary causal factor under such a view; such relations merely explain minor variations within a given morphogenetic field. The primary causal factor of every species is said to be some underlying set of morphogenetic processes embodied in a field which causes organisms in the species to have the form they exhibit.

Process Structuralists envision a morphological landscape similar to the epigenetic landscapes in Waddington (1940). Peaks in a morphological landscape represent developmentally stable morphologies. Extant morphologies come about through transformations from ancestral peaks. These tranformations are mapped out by generative or transformational laws. By specifying initial parameter values for a morphological landscape, Process Structuralists believe they can derive all the possible descendant morphologies for any extant (ancestral) morphology. In this way Process Structuralist believe they can offer a better prediction of future evolution and a better test of phylogenetic hypothesis than neo-Darwinians.

Process Structuralists also claim that the emphasis on developmental processes will enhance biology's explanatory power. They revere universal generalizations and reject explanations based on historical contingency. They propose what they call a "Kantian" understanding of scientific theory structure: Smith (1992) gives the following synopsis of the Kantian nature of the Process Structuralist approach:

> "Under such a view, a given process is only intelligible if it proceeds in accordance with a formal rule. In the context of biology, these formal rules or generative laws are to be embodied in decidible deterministic equations." (Smith 1992, p. 434)

Process Structuralists believe that since neo-Darwinism is driven by stochastic processes such as mutation and drift, it is resigned to offer unintelligible explanations. Process Structuralists advocate replacing neo-Darwinian stochastic mechanisms with formal laws whenever possible. The problem they have with neo-Darwinism is that it treats genetic processes as inherently random, as such the processes fail to be proper subjects of general laws. Hence, Process Structuralists argue that neo-Darwinian mechanisms such as variation and selection should take a back seat to generative/developmental mechanisms. Smith (1992) notes that the Process Structuralists aim to unify all of biology, evolutionary theory and developmental theory, with formal laws.

Process Structuralists see generative laws much in the same way as laws within physics, such as Kepler's laws concerning planetary motion. A small set of laws circumscribe a set of possible morphologies. Moreover, homologous motions (i.e. stability regimes) can result from rather different initial values, indicating that an atomistic approach (i.e. trying to explain the difference in terms of a single value) to understanding homologous motions is doomed to failure. Understanding the complexity of the interactions is required to understand the nature of the homologous motions. This does not mean that selection and genes are unimportant in evolution. However, they do take on a secondary role. They are useful for identifying local parameters of the generative laws.

As with all the other approaches to understanding species, Process Structuralism faces some problems as well. At a quick glance it appears to suffer from the subjectivity problem that plagues any phenetic species concept. For example, it seems plausible that different groups of biologists can highlight different morphological characteristics and hence develop radically different morphological landscapes. How is one to determine which morphological landscape is correct? Process Structuralists suggest that the way out of this problem is to posit generative laws for each peak in a morphological landscape and then experiment to determine which laws (if any) withstand testing.[41] Process

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[41] See Webster and Goodwin 1996, pp. 94-100.

Structuralism does not fall prey to the subjectivity problem which plagues the phenetic species concept because, unlike a phenetic approach to species, Process Structuralism attempts to offer a causal account of the identified groups of forms that make up species taxa in the biological classification.

There are other problems facing the Process Structuralist account. Griffiths (1996) has suggested that all the developmental mechanisms offered by Process Structuralists can be couched in terms of neo-Darwinian selection. Smith (1992) argues that much of the force of the Process Structuralist attack on neo-Darwinian explanations is taken away if we accept a schematic conception of the theory of natural selection. Although these are important concerns, in Chapter 4 we will find that they derive most of their strength if one presupposes the primacy of a neo-Darwinian approach. All in all, a Process Structuralist approach is not as controversial as it is made out to be by its critics.

Whether or not non-Darwinian views of species are legitimate is of great interest. Non-Darwinian species concepts, such as a genetic species concept or a Process Structuralist species concept, raise the possibility of a species pluralism that covers a wide range of biological processes yet includes species that exhibit different ontological statuses. Such a version of species pluralism has the benefit of covering many biological interests, but it appears to suffer from what we will call theoretical discord.

IX. Summary

As we have seen the species problem is rather formidable; no single species concept appears able to adequately handle all the biological situations that can be said to maintain discrete and stable groups of organisms biologists identify as species. All of the neo-Darwinian species concepts; the biological species concept, Van Valen's ecological species concept, the evolutionary species concept, and the history-based phylogenetic species concept, aim to explain the discreteness and stability of groups of organisms. However, none of these species concepts has the same understanding of the causal process that gives rise to species. Things get even more complicated when we consider non-Darwinian species concepts. As a result, it would appear that species monism is problematic.

Although one might object that biology ought to aim to reduce each of these concepts to a single species concept, each of the concepts we have examined (except for the phenetic species concept and possibly the genetic species concept) appears to reflect an important causal process (or processes) that can be said to maintain discrete and stable groups of organisms. As a result, species pluralism seems an appropriate stance. It is important to note that we are suggesting that species pluralism is required and that it is here to stay. The underlying biology of the groups of organisms biologists call species requires that they take a pluralistic approach. This will not change as we gain more knowledge. Species pluralism is here to stay because the underlying biology of species dictates that biologists be pluralists with regard to species.

Hull has proposed an ontological reconceptualization of species in order to explain the intractability of the species problem as well as provide reasons for pursuing a monistic solution with a neo-Darwinian flavor. He suggests that species be thought of as individuals instead of as classes with members. He argues that evolutionary theory actually requires such a view of species. This new ontological outlook requires that biologists reconceptualize biological taxonomy completely; it would appear that the traditional Linnaean taxonomic outlook is inconsistent with the view that species are individuals since the Linnaean taxonomy utilizes classes to organize the world's organic diversity.

As we have seen in this chapter and will continue to see, Hull's insistence that evolutionary biologists remain species monists appears misguided. However, if he is right about species being individuals, it would appear that evolutionary biology has reason to reject any approach to species which allow species to be classes. Hence, the individual/class issue appears to have an impact on the structure of any account of species pluralism that evolutionary biologists embrace. In the next chapter we will explore whether species really do need to be viewed as individuals. We will find that in a certain sense species do need to be viewed as individuals from a neo-Darwinian perspective. Let us now consider this more philosophical problem (i.e. the ontological species problem) regarding the nature of species and examine how, if at all, an answer to this problem serves to limit the types of species concepts within an account of species pluralism.

CHAPTER 3: THE ONTOLOGICAL SPECIES PROBLEM

Faced with the intractability of the species problem, some neo-Darwinian biologists and philosophers of biology have suggested that from an ontological perspective particular species are really individuals instead of classes with members. Neo-Darwinian biologist Michael T. Ghiselin (1974, 1987) and neo-Darwinian philosopher of biology David Hull (1976, 1978, 1987) have been the main advocates of this proposed ontological reconceptualization of species. They believe that getting clear about the ontology of species will provide at least a partial, if not complete, answer to the species problem. Both Hull and Ghiselin are advocates of the biological species concept. They believe that the biological species concept is the only concept that truly fits with the idea that species are ontologically individuals. We will call the debate surrounding the question of the ontological status of species *the ontological species problem*.

Consideration of this problem is relevant to this dissertation because Hull and Ghiselin believe that the only legitimate species concepts are ones consistent with the idea that species are ontologically individuals. One might attempt to use this idea to rule out certain species concepts. For example, since non-Darwinian species concepts appear to be in conflict with the idea that species are individuals, Hull and Ghiselin suggest that these species concepts ought to be rejected. In this chapter we will examine the ontology of species in order to determine what impact the ontological species problem has on species pluralism. We will conclude that the ontology of species is determined in large part by one's theoretical leanings.

It is important to understand that this ontological problem is distinct from the species problem examined in Chapter 2. Regardless of how species are to be picked out by biologists, it is a separate question to ask how species are to be understood *ontologically*. The species problem involves a debate about the defining criteria biologists ought to use to pick out species *empirically*. As we have seen, there are numerous definitions that have been offered and there appears to be no clear consensus on which definition is *the* correct one. The ontological problem involves a debate about the metaphysical nature of the concept "species" as it is used by evolutionary biologists. In terms of a question, we might understand the ontological problem to be asking whether we should view species as if they were either individuals with organisms as parts or rather classes with organisms as members. Such a debate is separate from the debate over which definition evolutionary biologists ought to use to pick out each particular species in the biological world. So, regardless of the definition we may accept as a solution to the species problem, we still may debate whether or not species (as picked out by our accepted neo-Darwinian or non-Darwinian criteria) are really individuals, classes, or perhaps some other ontological entity.

Those who hold that species are individuals have been said to advocate the *species-as-individuals thesis*. Basicially, the thesis is just as follows; *species ought to be understood ontologically as individuals consisting of parts instead of as classes with members*. In this chapter we will examine the two most serious arguments in favor of the species-as-individuals thesis; the *No Lawlike Generalizations* argument and the *Evolutionary Term* argument. The No Lawlike Generalizations argument holds that since biologists have not been able to develop general laws about each particular species that is recognized, each particular species name is best understood to pick out an individual instead of a class because this best explains why there are no general laws about species.

The Evolutionary Term argument holds that acceptance of evolutionary theory actually requires, in some sense, that each particular species be understood as an individual instead of as a class with members.

As we examine and critique the arguments in favor of the species-as-individuals thesis, we will find that it does make sense from a neo-Darwinian perspective to view species as if they were individuals of sorts. Much of the debate over whether species are individuals or classes has been fueled by Kitcher (1984a, 1984b, 1987, 1989). Kitcher argues that species need not be individuals. Sober (1984a), Hull (1987) and Ghiselin (1987, 1997) aim at rejecting his position. We will follow the exchange between Kitcher and Sober, Hull, and Ghiselin and find that there are some biological situations that appear to warrant viewing species as if they were natural kinds consisting of classes with members. In light of this, we will conclude that the ontology of species is determined (1) by the biological situation under investigation and (2) by the theoretical background of the investigator. The latter conjunct of this conclusion is not something most evolutionary biologists embrace. This is because most evolutionary biologists are neo-Darwinians. However, in the last chapter when we examine various accounts of species pluralism we will find that attempting to limit type of acceptable species concepts to those that only view species as individuals is a bit shortsighted and not good for biology overall. Before diving into the main arguments offered in favor of the species-as-individuals thesis, let us briefly examine what philosophers and evolutionary biologists have in mind when they use the term 'class' or 'individual' in biology.

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I. Basic Differences Between Classes and Individuals

Philosophers and biologists have traditionally thought of species as consisting of classes of individual organisms. Every species, such as *Homo sapien*, has traditionally been viewed just like any other class such as the class denoted by the term 'chair.' Traditionally, classes like *Homo sapien* and 'chair' have usually been taken to denote a class of objects. Objects have been assigned to each class according to some specified intensional definition of *Homo sapien* and 'chair.' These classes are in stark contrast to individual entities such as the Queen of England herself and the particular chair the Queen of England sits upon while on her throne.[1]

Hull (1976, 1978) offers a good analysis of the difference between individuals versus classes, and he has been a staunch defender of the species-as-individuals thesis. He suggests that individuals have a spatiotemporal location and are made up of spatiotemporally located parts. The parts of an individual do not need to be similar in any respect. Individuals exhibit some sort of cohesion or organization among their parts. Furthermore, individuals are thought to be described, not defined. The name of an individual is merely a marker, it carries no intensional meaning. Classes, on the other hand, have members, not parts. Members of the same class are members because they are thought to share one or more properties. These shared properties form the basis of the intensional class definition in terms of necessary and sufficient conditions.

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[1] It would appear that species were traditionally viewed as classes in large part because of the scientific methodology of the time. The prevailing scientific method in biology prior to the Darwinian revolution had been to place entities into classes based on the belief that similar looking organisms shared the same essential nature. Only since the 20th century did biologists become seriously interested in giving a causal account of what makes the organisms similar that was non-essentialist. See Hull (1989, Chapters 2 and 4) for further details.

One of the basic differences between individuals and the classes, then, is that individuals are spatiotemporally localized whereas classes are not. Classes do not need to have members at every given moment in time. The members of a class may expire or go out of existence at one point and come back into existence at a later time. All that is required for membership in a class is that the intensional definition of the class is met. Individuals, however, because they are spatiotemporally located must have a beginning and ending both in space and in time.[2] Once an individual goes out of existence, it is gone forever.

There is another important difference between individuals and classes to note. Individuals are named and the name's main function is to pick out the individual from among other spatiotemporal individuals. On the other hand, as already noted, classes are typically intensionally defined.[3] As mentioned already, the definition specifies the conditions for membership in the class. Anything that meets the conditions of the intensional definition, no matter where it is located spatiotemporally, is properly considered a member of the class.

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[2] Actually this is not necessarily true since metaphysically it seems possible for an individual to live forever, although the types of individuals we are used to dealing with (e.g. humans) all have endings. It would appear it is also metaphysically possible for an individual to exist without a beginning, though such a possible individual is clearly not under consideration here.

[3] Actually, classes need not have members that have anything in common. Kitcher (1984a, 1984b, 1987) points this out but, as we will see, his point is made with the aim of showing species can be classes in the sense of being sets. The above comments about the nature of classes captures the standard view of classes as used in conjunction with species.

II. Essentialism and Natural Kinds: The Received View of Species

The idea that species are classes has been prominent throughout the history of biology from Aristotle up to the 20th century. The Linnaean hierarchy, traditionally used to classify organisms, is grounded in the idea that species taxa are classes. Linnaeus expanded upon Aristotle's distinction between species and genus by recognizing five different classes; Kingdom, Class, Order, Genus, Species. Simpson (1961) and Mayr (1969) expanded upon the Linnaean hierarchy by recognizing twenty-one different classes. However many classes one decides to recognize, a few basic notions are shared by all Linnaean-like hierarchies. First, the hierarchy is understood to be a series of nested classes with the lower classes being subsumed under the higher classes. Second, each class is defined intensionally by indicating properties shared by members in the class. Lower classes like 'species' are given more specific definitions since the members of species presumably have a lot in common. As one proceeds up the hierarchy, the definitions for each class become less and less specific.

Ghiselin (1997) points out that the term 'hierarchy' has at least two different senses that need to be distinguished. An *inclusive* hierarchy is one in which higher levels do include lower levels. An example would be the relationship between undergraduate and sophomore. 'Sophomore' is included in the notion of 'undergraduate.' The Linnaean hierarchy is an example of an inclusive hierarchy. An *incorporative* hierarchy is one in which higher levels indicate wholes of which lower levels are a part. An example might be the relationship between university, college, department, professor. An essential feature of an incorporative hierarchy is some degree of cohesion that unifies all the parts. The levels in an inclusive hierarchy do not exhibit cohesion between them.

Ghiselin notes this distinction in order to assert that traditional biological classification is best understood as an attempt to develop an inclusive hierarchy of the world's biological diversity. An inclusive hierarchy is consistent with the view that particular species are classes with members. Ghiselin argues that current taxonomic practice employs an incorporative hierarchy.[4] His argument, however, hinges on whether or not particular species ought to viewed as individuals. Ghiselin clearly believes species are individuals, but whether or not his belief is correct will be addressed below.[5]

The Linnaean hierarchy is part of a general essentialist outlook that aims to discover biological natural kinds. Essentialism regarding species is the view that each species has a nontrivial set of properties that all and only the members of the species possess.[6] In comparison, the periodic table is said to be comprised of natural kinds. Each element in the periodic table is intensionally defined in terms of microstructural properties. Consider, as an example, the scientific definition of gold. Something is gold if and only if it has the atomic number 79. Every entity in the set of gold things must have the atomic number 79. According to those who have advocated the Linnaean hierarchy, species are defined in much the same way. Although the periodic table and the

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[4] Recall from Chapter 1 the distinction between classification and systematization. Classification utilizes an inclusive hierarchy whereas systematization utilizes an incorporative hierarchy.

[5] As noted in Chapter 2, Ghiselin argues in favor of the biological species concept. As a result he believes that cohesion exists among species parts. This belief fits with the notion that biological hierarchies are incorporative. However, in light of the problems with solely accepting the biological species concept it would appear that we need not accept Ghiselin's argument that biological hierarchies are necessarily incorporative.

[6] See Hull (1976, p. 176), Rosenberg (1985, p. 188), and Dupré (1993, p. 53).

Linnaean hierarchy each share this *essentialist* approach, one important difference between them is that the latter is hierarchical whereas the former is not.

The discovery of natural kinds has been viewed as important in science since natural kinds allow for the construction of lawlike generalizations. On the traditional empiricist account of science, lawlike generalizations are used to give explanations and make inferences with certainty, they are usually universally true of necessity, and they are confirmed by positive occurrences involving natural kinds. For example, being able to say 'The Queen of England is a *Homo sapien*' has traditional been viewed as allowing one to explain why the Queen acted the way she did in terms of her being a member of *Homo sapien* and furthermore, as allowing one to infer properties of the Queen, other than the properties typically used to pick her out as a member of *Homo sapien*. Also, the fact that the Queen of England was born with an opposable thumb has traditionally been taken to lend credence to a law something like the following: All members of *Homo sapien*, necessarily, have opposable thumbs.

Realism holds that natural kinds exist independently of human inquiry. Natural kinds are typically viewed as indicating real divisions in nature. Although the confirmation of natural kinds faces difficult empirical and epistemological problems, classes of natural kinds are said to be distinguishable from mere logical sets of objects on the grounds that empirical regularities based on natural kinds support the postulation of general scientific laws. The reason an arbitrary set of things does not commit us to any real division in nature is that such a set fails to give rise to a legitimate lawlike generalization. Logically, a set can contain any number of odd, unrelated entities and still be considered a set, whereas natural kinds seem to require something further than mere membership in a set. Natural kinds, then, are classes of entities having membership criteria that are independent of human thought. The Linnaean hierarchy aims to classify such biological natural kinds.

In light of this brief discussion of essentialism, consider the difference between viewing species as individuals and viewing them as classes designating natural kinds. As mentioned earlier, individuals have a particular spatiotemporal position. Individuals are given proper names as a result of some type of naming or baptismal ceremony. Names lack traditional defining properties and thus lawlike generalizations cannot be developed about them. Individuals can and often do change over time. As a result, individuals need not have an essence. Furthermore, there need not be one defining feature of an individual. Although some individuals change very little over the course of their existence, most individuals change and develop over time (an admittedly extreme example of this is a caterpillar's existence). Additionally, although the parts of most individuals are spatiotemporally contiguous, the parts of individuals need not be (consider the United States).[7] Typically, however, all individuals have some sort of internal organization or coherence; the parts of an individual usually stay together (e.g. form a unified whole) and may even function together over time. All of these considerations support the idea that attempting to develop lawlike generalizations about

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[7] Although, it is hard to imagine how a biological entity can maintain a sufficient sense of individuality without maintaining spatiotemporal continuity among its parts. As an individual the U.S. achieves its coherence mainly through political ties but political structures are irrelevant and nonapplicable to biological entities. Even still, as we will see later in the chapter, some evolutionary biologists and philosophers offer weaker versions of the species-as-individuals thesis that do not require spatio-temporal continuity.

individuals makes little sense. It would appear that lawlike generalizations, in order to carry significance, must range over many individuals, not just one.

Kripke (1980) and Putnam (1975) have attempted to give an extensionalist account of natural kinds that is nonetheless essentialist in spirit. Basically, an extensionalist approach to natural kinds attempts to define kinds in terms of essential properties of which we may or may not have an accurate account. For example, instead of defining water in terms of its phenomenal properties, an extensionalist approach would define it in terms of the microstructural property (e.g. H_2O). Objects are part of the same kind if and only if they have the same essence, not because they meet some intensional definition.

What makes this approach so innovative and interesting is that Kripke and Putnam suggest natural kind classes can be defined *ostensively*. Class names are treated as rigid designators. One way of defining rigid designator is to say something is a rigid designator if it designates the same object in every possible world. For example, proper names are rigid designators. 'Charles Darwin' picks out the same individual in every possible world even though he might not have written *The Origin of Species* in every possible world. With regard to species names in biology, Kripke and Putnam hold that as we gradually come to understand more about species, we move from ostensive stereotypical definitions that have the character "something I know not what" to fully informed causal definitions that have the character "something I know full well."

From a purely philosophical point of view, troubles with any essentialist viewpoint have been noted by many philosophers in the 20th century. Wittgenstein (1953) suggests that many of the class terms in our language do not have such tidy, structured definitions. The words 'game' or 'chair' are typical examples of class terms to which we assign members. These class terms, however, do not lend themselves to clear definitions in terms of necessary and sufficient conditions. There does seem to be an important cluster of features that most games and chairs have, but this cluster of features is neither necessary nor sufficient for being a game or being a chair. Searle (1959) offers a similar analysis from a more traditional philosophical foundation.

Within philosophy of biology proper, Hull (1981), Wilkerson (1993), Dupré (1993), and Ghiselin (1997) have viewed the extensionalist proposal of Kripke and Putnam with suspicion. The suspicion comes from believing that species are really individuals, not natural kinds. Those who support the species-as-individuals thesis hold that species names are defined ostensively which is usually done by the act of pointing to the entity and calling out a name.[8] Advocates of the thesis claim there are not any hidden species essences that need to be uncovered. As we will see, acceptance of this view of species would require modification of our understanding of the standard view of biological classification. Let us now analyze some arguments in favor of the species-as-individuals thesis and assess whether the thesis ought to be accepted by contemporary evolutionary biologists.

III. Arguments for the Species-as-individuals Thesis

Ghiselin (1974) and Hull (1976, 1978) offer an important series of arguments in favor of viewing species as individuals. Kitcher (1984a), Rosenberg (1985), and Dupré

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[8] Hull has been accused by Kitts and Kitts (1979) of falling into the extensionalist camp because of Hull's claims that species names are actually proper names. Kitts and Kitts interpret Hull to be admitting that species names are extensionalist rigid designators that refer to some real essence. Hull (1981) denies this by suggesting that an extensionalist view is irrelevant to the individuality of species.

(1993) all summarize the arguments given by Hull and Ghiselin in slightly different ways. Kitcher identifies three arguments; one which claims construing species-as-individuals is necessary in light of species evolution, another which claims species should be viewed as individuals because doing so explains why there can be no laws regarding species, and a third which claims that species must be individuals because species are historically connected. Rosenberg also identifies three main arguments but describes them differently than Kitcher. Rosenberg suggests one argument claims that treating species as individuals clears up the notion that species evolve, a second claims that species are really analogous to individuals in many respects, and finally a third claims that treating species as individuals shows why it has been impossible to formulate general laws about species. Dupré identifies five different arguments which essentially fall in line with the arguments identified by Kitcher and Rosenberg.

Kitcher, Rosenberg, and Dupré all seem to independently identify two main arguments in favor of the species-as-individuals thesis. The first will be dubbed the No Lawlike Generalizations argument, the second will be dubbed the Evolutionary Term argument. Both of these arguments carry the most weight and play important roles in the attempt to reconceptualize species ontologically as individuals instead of as classes of kinds.[9]

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[9] Although the species-as-individuals thesis has captured the attention of many biologists and philosophers, we will see that there are some problems with calling species individuals. This has prompted some to propose weakened versions of the species-as-individuals thesis. We will examine these versions shortly, but first, we will examine the two main arguments offered in favor of the species-as-individuals thesis.

The No Lawlike Generalizations argument

In its basic form the No Lawlike Generalizations argument suggests that species are individuals because only this can explain the apparent fact that no general scientific laws have been formulated about species. Recall that on the traditional empiricist account of science, scientific laws are understood as universal generalizations that are (1) necessarily true in virtue of the way the world is and (2) confirmed by positive occurrences involving natural kinds. A simple version of the No Lawlike Generalizations argument runs something like the following; since all the purported laws that have been offered about particular species turn out false, species are not natural kinds. Therefore, species must be individuals. An important presupposition of this argument is that species can only be one of two things; either classes or individuals. As we will see near the end of the chapter, this presupposition has come under recent scrutiny.

This simple version of the No Lawlike Generalizations argument allows us to easily identify this presupposition, but it is important to note that an argument as stark as this simple version is not advanced by all advocates of the thesis. Hull (1976, 1978) does mention that no lawlike generalizations regarding species exist, but he is arguably understood as using the notion that species are individuals to *explain* why there are no such generalizations.[10] He suggests that the truth of the statement "There are no lawlike generalizations about species" should not be surprising since the following statement is true, "Species are really individuals." Kitcher (1984a) interprets Hull as *concluding* that the species-as-individuals thesis should be accepted because the thesis helps explain why there are no general laws about particular species; in essence, Kitcher views Hull's

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[10] Sober (1984a, p. 338) points this out.

position as one that uses the *explanatory import* of the species-as-individuals thesis as *evidence* in favor of the thesis.

The idea that there are no lawlike generalizations regarding particular species *prima facia* appears to support the claim that biology is not a genuine science as advanced by Smart (1963). Even though they support the species-as-individuals thesis, Hull (1987) and Ghiselin (1987, 1997) reject the idea that biology is not a science. Part of their reason for doing so stems from their belief that descriptions are an important part of any science. Laws alone do not make a science. Evolutionary theory appears to contain laws which govern all biological organisms including species. Particular species, like *Felis domestica* or *Homo sapien*, fall under these laws. However, instead of developing laws about particular species, Hull and Ghiselin believe biologists should be developing detailed, descriptive statements about particular species. Such detailed, descriptive statements take the form of historical narratives which are much like a biography of a person. Historical narratives offer a somewhat different but nonetheless important basis for explaining and predicting the behavior of particular species; as the narrative becomes more complete it provides a better basis for saying that a certain evolutionary change within a species was expected or even that a certain evolutionary change is likely given what a species has done in the past. Again, the analogy with a biography is instructive. Given what we know about how a professor has graded over the past twenty years, we are able to predict how the professor will grade on his upcoming final exam. Furthermore, there is a sense in which we get an explanation of the grades given out on the final exam by appealing to how the the professor has graded over the past twenty years. Hull points out that other narratives like a description of the rise and fall of the Third Reich are explanatory. For example, such a narrative might help explain why Germany has the political structure it has today. Both Hull and Ghiselin hold that narratives of particular species function in much the same way to explain and predict the development of particular species.

The No Lawlike Generalizations argument attempts to show that the fact there are not any laws about particular species should not be perplexing since the idea of developing laws about particular individuals does not make much sense. However, this does not necessarily support Smart's claim that biology is not a science. Hull and Ghiselin's account of the role of descriptive statements and historical narratives in evolutionary theory is committed to an account of scientific explanation which does not involve making an inference from a law. Hull and Ghiselin both reply to Smart's criticism of biology by suggesting that even though biology does not always utilize lawlike generalizations when giving an explanation of species, biology ought to still be considered a legitimate science because historical narratives ought to be considered just as explanatory. As a result, the No Lawlike Generalizations argument supports the claim that evolutionary biology, at least with regard to its understanding of species, is not open to Smart's criticisms.[11]

Related but distinct issues

There are a host of issues surrounding this argument that need to be carefully distinguished from the issue at hand. Recall that we are interested in *evolutionary* biology in this dissertation; specifically, we are interested in how evolutionary biology

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[11] Of course, Smart's criticisms of biology would also need to address the possibility that there are other parts of biology, such as laws about types of species, which do function as classes about which there can be laws.

understands and identifies species. Regardless of what we conclude concerning this issue, it may well turn out that there are legitimate lawlike generalizations within other areas of biology. Consider the Hardy-Wienberg Law of population genetics which can be characterized as follows:

> "If there are p A genes and q a genes at some locus in a population, then the frequencies of the three genotypes AA, Aa, and aa will be p^2, $2pq$, and q^2, respectively."[12]

In addition, consider Fisher's Law concerning the sex ratio. Basically, this law states that natural selection will produce an even ratio of males to females whenever mating is random. Although these may be legitimate laws of biology, and even evolutionary biology proper, their existence does not answer the question concerning whether there are laws regarding particular species.[13]

Some have suggested that even though there are laws in biology, biological laws have a special form distinct from other scientific laws such as those in physics. For example, Sober (1993) and Brandon (1997) suggest that biological laws are more properly seen as "models" which are nonempirical, much like mathematical truths. This is in contrast to the laws of physics which are empirical. Although Sober and Brandon characterize biological laws as nonempirical, both suggest that biological laws have lawlike characteristics. Still, even if this distinction between the laws of biology and the

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[12] From Sober (1993, p. 71) P and q are place holders for any given number or numbers.

[13] Certainly it would appear that the Hardy-Weinberg Law is utilized by evolutionary biology, however this does not make it a law of evolutionary biology *per se*. Whether it is a law of *evolutionary* biology is part of a larger issue concerning what the structure of evolutionary theory is. See Rosenberg (1985, 1994) and Sober (1984b, 1993) for more about this rather large issue. For the purposes of this dissertation, at the very least it seems clear that the Hardy-Weinberg Law is not a law that concerns the nature of species directly.

laws of physics can be borne out, this issue is separate from the issue concerning whether there are laws regarding particular species.

The issue raised by the No Lawlike Generalizations argument is whether evolutionary biology can develop legitimate lawlike generalizations regarding particular species or whether evolutionary biology is limited to offering detailed descriptions of particular species. Note that the issue we are addressing may not resolve whether evolutionary biology is solely a nomothetic or solely an historical science since even if we find that there cannot be laws regarding individual species, laws such as the Hardy-Weinberg Law and Fisher's Law may still be viewed as legitimate lawlike generalizations. However, our resolution of the species laws issue does have an impact on how we view biological taxonomy. If there are no laws regarding individual species, then our taxonomic hierarchy of biological organisms is best understood as an in-depth historical narrative rather than a nested hierarchy of classes. In which case, it would appear that the taxonomic hierarchy is incorporative and systematic in nature rather than inclusive and classificatory.

Evaluation of the No General Laws argument

Kitcher (1984a, 1984b) has objected to the explanatory variant of the No Lawlike Generalizations argument on the grounds that he believes lawlike generalizations can be developed about particular species. By taking this position, Kitcher responds to Smart's criticism of biology a bit more directly than advocates of the species-as-individuals thesis. Kitcher agrees with Smart and Hull that apparent lawlike statements about species such as "All platypus have flat, leathery snouts" are not legitimate scientific laws; the reason being that such statements are mere contingencies that easily could have turned out false or could easily turn out false in the future. Kitcher suggests that biologists are not surprised when biological generalizations about particular species turn out false because evolution works in such a way that exceptions to the rule are to be expected. In spite of this however, Kitcher argues that biological laws regarding particular species are not impossible. He discusses the possibility of uncovering laws about the developmental systems of various species. Suppose we found that the developmental system of organisms in a species could not be disrupted without one of two events happening; either inviable zygotes are produced or instantaneous speciation occurs. He suggests that it is possible to construct laws concerning the disruptability of the developmental features of species. As a result, Kitcher concludes that the species-as-individuals thesis is not supported by the claim the that scientific laws about species are impossible; he believes his example shows such laws are not impossible.

Sober (1984a) rejects Kitcher's proposal for possible laws about species on two main grounds. First, Sober suggests that the inviability of offspring does not make the offspring part of another species. Inviable zygotes are still members of the population they are born into and if they are part of the population, then they are part of the species. So, Sober denies that the first potential result of a disrupted developmental system, namely the production of inviable zygotes, marks a species boundary. Secondly, Sober suggests that there can be no condition or character that is so essential to the nature of a species that its disappearance or failure to be expressed in future offspring would result in instantaneous speciation. He suggests that *determination* of speciation, and consequently the naming of species, is always retrospective. It cannot be determined at the moment of offspring production. He underscores this point by considering the difficulty of determining the founder group of a new species as discussed by Mayr (1963). Sober says,

> "Suppose a flood separates a small number of isolates from the main part of the population. Selection leads this group to diverge from the parent population, and thereby to count as a distinct species. When did this new species come into existence? One natural answer is that it began at the time of the isolation event, even though the isolated organisms may have been no different from the organisms in the main population. The founders were founders of a new species precisely because of what happened later, and not in virtue of anything special about them. In the same way, an offspring may be as different as you wish from its parents. Whether it falls into a new species depends on what happens later." (1984a, p. 339)

So, Sober concludes that the possibility of laws about species cannot be grounded in the idea that disruptions in the developmental process can result in nearly instantaneous speciation. Hence, he claims Kitcher's desire to hold out for the possibility of scientific laws regarding species is misconceived.

In reply to Sober's criticisms, Kitcher (1984b) makes two claims about the attempt to argue in favor of the species-as-individuals thesis in light of there not being any scientific laws about species. First, he claims that the real explanation for there being no such laws about species does not lie in the fact that species are individuals. Rather it lies in the fact that the properties typically chosen to distinguish organisms as being part of a species "could all too easily have been missing in some members of the species" due to mutations or different pairings of gametes. So, in a way, Kitcher feels biologists have been looking at the wrong aspects of species when attempting to formulate general laws about them. As a result, advocates of the species-as-individuals thesis do not give the right explanation for the fact that there are no scientific laws about species.

Secondly, and more importantly, Kitcher claims that the possibility of there actually being laws should be left open and he claims Sober misinterpreted his description of how such laws might occur. Kitcher attempts to clear up the confusion by suggesting, more precisely, two possibilities for biological lawlike generalizations about how much change is allowable within either the developmental process or the genome of organims in a species.[14] The first possibility is the existence of *prohibitive* laws pertaining to the developmental process of organisms of a species. During the process of gamete formation it is possible that the process can go awry if certain properties are not produced or if they fail to be passed on to the offspring. Such a possibility suggests that certain properties are so deeply constitutive of various species "that attempts to eliminate them from descendants inevitably fails." (1984b, p. 622) Such prohibitive laws about particular species would indicate properties that cannot be left out during the developmental process of the organisms in a species.[15] The second possibility for scientific laws deals with the occurrence of polyploidy. Kitcher suggests that laws about the chromosome number and structure can possibly be formulated for species in which polyploidy is a serious possibility. Presumably he believes the rather sudden chromosomal change that takes place in cases of polyploidy can serve as a natural measure of species boundaries.

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[14] Kitcher's suggestions concerning laws for species represent just two possibilites. Certainly we might consider other possibilities for species laws such as shared phenotypes or shared adaptations among species members. However, Kitcher's two suggestions seem as plausible if not more plausible than these other possibilities.

[15] Such laws need not be prohibitive, since they could read something like this; "All members of species *x* must exhibit (c_1, c_2, c_3....) types of properties and they must partake in (p_1, p_2, p_3....) types of processes during the developmental stage."

Sober's suggestion that species determinations are always retrospective seems to conflict with Kitcher's (*) principle which was discussed near the end of Chapter 2. Recall that the (*) principle holds that a proposal to call the parts of a lineage a species should only depend on the properties and relations *intrinsic to the parts in the lineage in question* and not on the properties and relations of parts of other lineages (future, concurrent, or past). Sober seems to ground claims about species determination on incomplete empirical evidence regarding actual splittings. But in light of the acceptability of the (*) principle, this seems somewhat less than desirable.[16]

In order to get a better understanding of why Sober's grounds for species determination are less than desirable, consider the following. It would seem reasonable to suppose that most "hopeful monster" offspring which deviate radically from the normal developmental processes of a particular species simply die before anyone gets a chance to see them. Now, if we had access to knowledge regarding what types of offspring do not survive, this information would appear directly relevant to our determinations of what count as species. Kitcher's first suggestion that there are prohibitive laws regarding the limits of change within species seems to be asking whether a more immediate empirical foundation can be given for our claims about species determination. The mere fact that biologists currently determine species retrospectively seems irrelevant. Kitcher's point seems to be that if there is additional immediate evidence which would help our species determinations, we ought to seek ways to obtain that evidence. Furthermore, although reflecting a somewhat different biological

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[16] Of course we may have to occasionally settle for such retrospective determinations when we have little evidence but this is merely a practical point. The real issue is

situation, Kitcher's second suggestion concerning laws pertaining to the production of polyploid offspring might provide a basis for developing laws about species that falls in line with Kitcher's (*) principle. Polyploidy certainly involves a radical restructuring of the parental genome. Such an event would appear to be a significant biological occurrence. As a result, the development of polyploid individuals might be taken as an immediate violation of a species specific law regarding how much change in the genome can occur before a new species is produced. Such a law would not require biologists to see how things turn out before naming a species. It is worth noting that polyploidy is not a rarity. Ridley (1996) points out biologists estimate that about 50% of flowering plants were hybrids created through polyploidy.

It is worth considering more closely what Kitcher means by *possible* when he suggests that radical changes in the developmental process or the genome of organisms in a species will not be possible without resulting in either inviable zygotes or the creation of offspring of a new species. Kitcher suggests that attempts to remove deeply constitutive properties from the developmental program of a species will fail because such moves are biologically impossible.[17] We can interpret Kitcher as suggesting that laws regarding what is *biologically possible* for each species's developmental program

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whether we can find a better foundation for our determinations. Acceptance of the (*) principle would seem to at least commit us to pursuing such a foundation.

[17] Incidentally, Kitcher's position appears to bear some similarity to the Process Structuralist approach that we examined near the end of Chapter 2. Recall that Process Structuralists aim to explain diversity by identifying morphogenetic processes or transformations which dictate the forms which organisms exhibit. According to Process Structuralists, biology must develop a taxonomic scheme aimed at discovering laws of transformation which govern natural kinds. Hence, they attempt to develop a theory of evolution that is consistent with species being natural kinds. Also, Kitcher's position seems to bear some similarities to Kauffman (1993)

might be codifiable in some type of biological law. Some moves are biologically impossible in the sense that they do not result in organisms which are viable. Hence, Kitcher suggests that biologists might be able to identify certain properties of each species's genome that must not be tinkered with.

Problems with Kitcherian Species Laws

Having a solid understanding of Kitcher's notion of biological impossibility allows us to easily highlight a number of potential difficulties with it. One problem for Kitcher concerns whether such laws will actually reflect the distinctions between the various species recognized by biologists. The use of developmental programs as a basis for laws about species may not be a fine-grained enough measure to delimit all the species currently recognized. Many species share common developmental programs. In light of this, rather than marking *species* boundaries, the general laws that Kitcher speaks of might merely mark laws about higher level taxonomic groups. Such laws might legitimately indicate something like the general types of potentially viable offspring that could occur, or to put it another way, the laws might indicate what types of body plans/forms are viable. However, body plans/forms may not provide a sufficient foundation for labeling the various groups of discrete and stable organisms in the world as species.

A related problem for Kitcher is that the laws dictating the types of change available to an organism might actually reflect more fundamental physical or chemical laws regarding the types of geometrical shapes that are physically possible. If this were so, the laws Kitcher hopes to hold out for would not really be laws of biology. Instead, the groups of organisms identified as species by biologists would be identified not because of anything particularly biological but rather because of deep underlying lawlike physical/chemical processes. Beatty (1997) appears to embrace this type of view when he argues that there are no laws in biology. He attempts to show that all purported lawlike generalizations about the organic world are either deductive consequences of some lower-level physical/chemical laws or mere biological contingencies. Part of his evidence for this is that all purported biological laws either turn out to have counterexamples or they fail to be sufficiently necessary. According to his view, the laws governing the Library of Mendel would be physical/chemical laws, not biological ones.

Kitcher (1984a, p. 315) does offer a skeleton response to this objection in a rather incomplete footnote (#11). Kitcher says he aims to stay agnostic on the issue of whether species have non-trivial essences. His motivation for staying agnostic is his belief that not all scientific explanation need involve derivation from some law. As a result Kitcher claims that although species may be sets of natural kinds, these kinds need not form the extension of a predicate in a biological law. Kitcher's position may seem strange at first, but it is somewhat more understandable when we get a better understanding of his view of scientific explanation.

Kitcher (1981, 1989) advocates an explanatory approach that downplays the roles of exceptionless general laws and instead attempts to unify our scientific beliefs under the least amount of argument patterns that can serve the functions of science. In its basic form Kitcher's explanatory unification approach can be described as follows; given a set of at least two or more statements, an explanatory approach is more unified and hence more deserving of use than another explanatory approach if and only if it can derive more statements in the set using the least amount of statements in the set in conjunction with the least amount of argument patterns.[18]

Kitcher's position is similar to the traditional empiricist approach to explanation in that he also requires explanation to involve deducing the thing to be explained from other statements. However, one important difference between the two approaches is that the explanations under Kitcher's approach do not require general laws *per se*. The force of the explanation stems from unification of our beliefs through the use of argument patterns, not general laws. As such the arguments used by scientists do not need to use general laws. As a result, the claim that the laws about species offered by Kitcher are not general would appear to be irrelevant since general laws would not be necessary for good scientific explanations.

Although this approach appears to offer Kitcher a way of answering the criticisms raised by Beatty's position, it is not clear that a unification approach will be of much help to the issue under consideration. The big question for Kitcher's laws about species seems to be whether argument patterns that utilize such exception-ridden, spatiotemporally grounded "laws" will figure into a set of argument patterns which is sufficiently unificatory. It might be more likely that argument patterns which utilize Beatty's physical/chemical laws as premises would provide better unification of our beliefs.[19] Hence, the fact that the laws about species are not very lawlike would still be an issue.

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[18] Klee (1997) gives a good summary of Kitcher's explanatory unification approach. The account given here leaves out the technical notion of stringency when defining unification. Although important, it is not required for the purposes of this brief discussion of Kitcher's approach.

[19] This might be due to the fact that argument patterns with more lawlike premises are less stringent. See Kitcher (1981) for details on stringency.

We might try one last avenue to save the claim that there are laws about species. We might consider whether particular species laws can be developed that are probabilistic or stochastic in nature. For example, Sober (1984b) suggests that the principles and laws of evolutionary theory cannot be used to determine *with certainty* the outcome of evolutionary events. Rather, evolutionary biologists must be content with calculating the relative probabilities of a number of possible outcomes. Applying this probabilistic approach to species, it would appear that laws about individual species might be formulated in the following manner; "There is a high likelihood that any given member of species *x* will have property *y*." Such laws would appear to answer the criticism that there is no single property which is shared by all members of a given species.

The idea that there are probabilistic species laws is worth brief consideration. There might be an important similarity between probabilistic laws in physics or chemistry or even in some other areas of biology and probabilistic laws concerning particular species. For example, laws concerning the decay of a molecule capture the notion that the rate of such a decay is highly indeterminate. Consider a biological example concerning the inheritance of genetic traits. Biologists expect certain trait outcome ratios from the parental crosses they make. However, these trait outcomes are merely probable. Of course the expected trait outcomes become more probable as the population size increases. It might be possible to develop particular laws about species that are indeed probabilistic. A potential problem with this approach is that such species laws may not have a sufficient degree of probability to make them worthy candidates for probabilistic laws. Of course if Kitcher is right, then highly probabilistic laws about particular species might be possible.

Ultimately, consideration of whether probabilistic laws concerning particular species are possible will not resolve the issue at hand. Whether the laws concerning particular species are probabilistic or whether they are regular general laws is an issue separate from the question concerning whether laws about particular species are possible at all. A probabilistic account of species laws will face many of the same difficulties faced by a regular general laws account of species laws. The biggest difficulty facing any account of laws regarding particular species is the neo-Darwinian idea that any species can exhibit unlimited change and still remain the same species. If this is so, then any account of species laws would appear to be doomed. There would appear to be no solid foundation for fomulating even probabilistic laws since species could conceivably change their entire complexion.

In light of the idea that species can exhibit unending change, a full account of laws concerning particular species looks difficult to establish. Even if we could iron out the problems regarding the lack of generality that such laws would exhibit, the question still remains whether such laws are really about species. Of course we could tow the line and hold out for the discovery of such species specific laws. After all, as was noted when the No Lawlike Generalizations argument was introduced, the argument is seen by many as merely offering an inference to the best explanation. We could reject the use of this inference to explain the lack of species laws and continue to search for species laws without suffering any logical inconsistencies. The inference to the best explanation argument form seems plausible only if we feel we are close to getting at the truth about the nature of the world. However, whether or not we are getting close to getting at the truth about the world, and species in particular, is still undecided.

As a matter of fact, advocates of Process Structuralism implicitly suggest that we reject the No Lawlike Generalization argument and aim to develop laws which govern species. However, the burden would appear to fall upon Process Structuralists to make such a rejection worthwhile. This would appear to require them to produce some set of useful species specific laws. Instead of pursuing this issue further right now, let us turn to examine a more formidible argument in favor of the species-as-individuals thesis, the Evolutionary Term argument.

The Evolutionary Term argument

Most biologists hold that the attributes of a species are mere contingencies; any species could lose any one of its attributes and still be the same species. Although we have seen that Kitcher thinks some necessary attributes can be found, most biologists believe evolution precludes such attributes *a priori*. Such a belief serves as the foundation for the Evolutionary Term argument. This argument for the species-as-individuals thesis appeals to the nature of evolutionary theory as evidence. Basically, the Evolutionary Term argument claims that in order for species to evolve, they must be individuals. Classes, it is argued, cannot evolve. Only individuals can evolve. Insofar as species are the units of evolution, species must be individuals instead of classes (which refer to natural kinds). Like the No Lawlike Generalizations argument, the Evolutionary Term argument presupposes that species can only be one of two things; either classes or individuals. After examining the Evolutionary Term argument, we will examine how this presupposition has come under scrutiny.

Arguments by Hull and Ghiselin

Hull (1976) offers some comments on the structure of evolutionary theory in support of this argument. Evolutionary processes occur at various levels and require continuity. These basic levels; genic, organismic, and species, are integrated by the part-whole relationship. Putting the matter dogmatically, Hull states, "*the* gene is *the* unit of mutation, *the* organism is *the* unit of selection, and *the* species is *the* unit of evolution." (1976, p 181). Mutations give rise to adaptations which are in turn reflected in the discrete and stable groups biologists recognize as species. Evolutionary theory cannot have a radical ontological break between the organismic level and the species level. Hull also suggests that regardless of what happens at the lower levels, evolution itself requires spatiotemporal continuity, the potential for open-ended development, and a sufficient degree of internal unity. Ghiselin (1974) takes a more direct tack. He argues that species result from two biological processes; gene flow and reproductive isolation. He goes on to suggest that these processes can only occur within individuals. Hence, he concludes that species must be individuals.

In a later article, Hull (1978) utilizes the lingo of phylogenetics and systematics a little more directly in his defense of the Evolutionary Term argument. He claims that acceptance of an evolutionary outlook requires biologists to utilize the notion of a lineage when identifying groups of organisms as species. Lineages, as defined by Hull, are ancestor-descendant copies of some original form (gene) that persists through time in some spatial location. Such lineages are formed through the continuous acts of replication and reproduction. Hull believes that in evolutionary terms the important units of evolution are lineages. Since he believes species lack sufficient cohesion (gene flow) to be units of selection, he argues species ought to be seen as the result of selective replication and reproduction among genes or organisms. As such, species are lineages of genes or organisms that evolve.[20] This version of his stance on species individuality reflects his consideration of the criticism that species are not often held together by gene flow. Hull identifies reproduction and heritable selection as necessary processes of species and then suggests that spatiotemporal locatedness and historical connectedness between the parts of a species is required in order for reproduction and heritable selection to occur within species. As a result, he concludes species must be individuals if they are to be able to exhibit the processes of reproduction and heritable selection.

A Set View of Species: Kitcher and Wilson

At the very least, the Evolutionary Term argument holds that evolutionary theory requires that species be viewed instrumentally as individuals (or more precisely, as historical entities). Kitcher (1984a, 1984b, 1987, 1989) argues against the Evolutionary Term argument because he feels viewing species as individuals is problematic in some biological situations. Falling in line with Rosenberg's comments in the previous section, Kitcher claims species *can* be arranged into biologically interesting *sets*. Instead of attempting to conceive of species as classes, he substitutes the notion of a *set* rejecting the

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[20] Wilson (1995) suggests that viewing species as lineages is actually an alternative to viewing them as individuals. His suggestion raises an interesting issue. On first glance it would appear that Wilson has mixed his ontological categories; 'individual' in the sense that Hull and Ghiselin have been using individual would appear to be a more broadly applicable concept than 'lineage.' However, as we will see shortly, 'individual' as a concept carries a lot of metaphysical and conceptual baggage that some feel is neither useful nor appropriate for biological situations. Wilson would appear to prefer the ontological category 'historical entity' over 'individual' when describing the ontology of species. Hence, on Wilson's view 'individual' and 'lineage' would be two different types of historical entities. We will examine the idea that species are historical entities below.

notion of a 'class' as a bastard, essentialist-laden notion foisted upon philosophers and biologists by an outdated Aristotelian paradigm.

Recall that the Evolutionary Term argument claims that classes cannot evolve. If we substitute the notion of 'set' for 'class,' Kitcher (1984a) argues this claim is false. He argues that the Evolutionary Term argument commits the fallacy of incomplete translation. Kitcher gives the following counterexample to make his point: "Curves have tangents. Sets of triple numbers are nonspatial entities. Hence sets of triples of real numbers cannot have tangents. Therefore curves are not sets of triples of real numbers." (1984a, p. 311) Kitcher points out that the correct way of responding to the counterexample is to say that "....in the reduction of geometry to arithmetic, the property of being a tangent is itself identified in arithmetical terms." (ibid.) He then suggests that the same sort of response is available to all variants of the Evolutionary Term argument. What deludes advocates of the Evolutionary Term argument into thinking that sets of organisms cannot evolve is their failure to translate completely; that is, they fail to see that the property of evolving can be identified in set-theoretic terms. Once this is recognized, Kitcher believes the Evolutionary Term argument should be viewed suspiciously.

Kitcher argues that rejection of essentialism is laudable but rejection of the set view of species is unnecessary. He believes the idea that species can be sets is not ruled out by the requirements of evolutionary theory. Kitcher fleshes out the idea that species can evolve while viewing species as sets in the following way:

> "For any given time, let the stage of the species at that time be the set of organisms belonging to the species which are alive at that time. To say that the species evolves is to say that the frequency distribution of properties (genetic or genetic plus phenotypic) changes from stage to

> stage. To say that the species gives rise to a number of descendant species is to claim that the founding populations of those descendant species consists of organisms descending from the founding population of the original species." (1984a, p. 311)

Although he does not give a detailed account, Kitcher believes it is possible to develop a set view of species which accurately reflects the genuine forces of evolution when calculating the fluctuations in frequency of various properties within a species.

Wilson (1991) offers a more detailed account of how one might view species as sets. In so doing he first points out that the question "Are species sets?" is ambiguous. He contends there are two related questions being asked in this question; one asks whether a set can be identified with each species, and another asks whether a species can be identified with each set. The first question is a question about sets; it assumes that we already have a conception of species and that we have used this conception to identify various particular species. The reason for asking this first question is to determine whether sets can be identified with the various groups of organisms we have already identified as species. The second question is a question about species; it assumes one has a sense of the various sets (i.e. sets of objects, sets of numbers, etc) that can be formulated. The reason for asking this second question is to determine whether species can be identified with the various sets that can be formulated. Wilson suggests that the answer to the first question is a qualified yes while the answer to the second question is a definite no.[21] Our concern will only be with the first question since, as Wilson claims, this is the question with which Kitcher (1984a) is originally concerned.

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[21] Wilson argues the answer to the second question is a definite no since it is silly to suppose a species can be identified with a set of infinite numbers or a set of inanimate objects. In light of this Wilson modifies the second question so that it asks merely whether a species can be identified with *some* sets. He argues the answer to this modified

In order to understand Wilson's argument a quick refresher on set theory might be helpful. There are two basic properties of all sets. First, sets have zero or more members. Second, the identity of sets depends solely on their membership. Furthermore, sets can be defined by enumeration or by a property shared by all the members. Every finite set is definable by a property. Even if there is no perceivable underlying causal property that underlies the members of a set, one can simply define the set in terms of a property by referring to the property of being a member of the set in question.[22] Assume the expression 'Fx' refers to the sentence form 'x is F'. 'F' in such a sentence form represents a single property, a conjunction of properties, or a disjunction of properties. Any set defined by a property must furthermore be well-defined in the sense that the property doing the defining must allow one to specify the members of the set.

As reflected in the Evolutionary Term argument, the biggest obstacle facing any attempt to identify a set with a species is the fact that species change over time. Advocates of the Evolutionary Term argument suggest that the identity of the species does not solely depend on the organisms that belong to it. Organisms can come and go and this does not affect the identity of the species. However, the identity of a set depends solely on its members; members of a set cannot come and go without the set identity

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version of the second question is no as well on the grounds that there are numerous set definitions one could use to pick out what we would consider a biologically interesting species. Some of these set definitions reflect our current biological knowledge but others do not. The problem is that there is not way to decide which which set definition is correct without referring to our current biological knowledge of species. Wilson argues that making such a reference means we actually begin to ask something like the first question, namely whether a set can be identified with a species.

[22] Kitcher (1984a) claims such a property is a property only in an "attenuated sense" of the term.

being affected. Hence, a set identified with a species at time t_n will be different from the set identified with the same set at time t_{n+1} assuming that the species has evolved.[23]

Wilson suggests the way around this problem is to define the set with a temporal dimension built into the definition. He suggests the following schema with the required temporal dimension to be used for identifying a set with a species:

(β) $S^* = \{ x : (\exists t) [O(x,t) \& F(x,t)] \}$

He gives the following description of the schema;

> "'S*' represents a set, 'x' represents a variable ranging simply over entities, 't' represents a variable ranging over all moments of time until the present, 'O' represents the property of being an organism, 'O(x, t)' represents x's having the property O at t, 'F' is understood as representing the property equivalent to a property that constitutes an analysis of a conception of the species in question and where 'F(x, t)' represents x having property F at t." (1991, p. 421)

He argues that such a schema allows for the inclusion of past and present organisms in a species and it allows for the inclusion of enough organisms of a species so that significant biological statements pertaining to the species in question can be given.

Wilson considers a few objections. One might object that since no defining properties of any species are possible, then an identification based on 'F' within schema (β) cannot be made. Wilson replies that one property that could be used is the property of belonging to the species in question. He claims, contra Hull and Ghiselin, the fact that such a property is merely a logical artifact of the use of a species name is irrelevant. Another possibility is to use a relational property like 'descending from a pair of organisms that are or were part of an interbreeding population.' Relational properties are

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[23] Sober (1984a) appears to be the first to formally raise this problem with a set view of species.

no worse candidates for defining properties than traditionally conceived essentialist properties.

Another possible objection is that significant biological statements cannot be developed from such identifications because species evolve. Such statements will always be changing. Wilson replies that nothing precludes biologists from identifying a different set with a species each time they decide to change the conception of a species, and in turn, changing the biologically significant statements. As he says "...the definition of the identified set should change as one's conception changes; as all conceptions, conceptions of species are hostage to the future." (1991, p. 424)

One might still object that the sense of "biologically significant" associated with such definitions is rather weak. This is because the definition of "biologically significant" as it pertains to statements about species appears to be directly related to the relative frequency of characters over time within a species and, as the objection goes, no characters are going to have a high frequency within any species after a long enough period of time has elapsed. There appear to be two replies to this obejction. First, Wilson's burden is not necessarily the same as Kitcher's burden which we examined earlier. Recall that Kitcher argued there is a possibility of discovering lawlike generalizations about each species. Wilson, however, need not commit himself to such a strong position. All he is suggesting is that evolutionary biologists can utilize a set view of species and they can temporarily identify species with an acceptable definition at the moment of investigation. Wilson need not commit himself to developing biologically significant statements that are lawlike in nature. A second reply one might offer in favor of Wilson is simply that the verdict is still out on the issue of whether there are lawlike generalizations for each species. Just because species evolve does not mean that there cannot be lawlike generalizations developed about them.

Wilson's argument gives life to the idea, first suggested by Kitcher (1984a), that species can be meaningfully viewed in set-theoretic terms. One could repeatedly use schema (β) to identify sets with stages of a species over a period of time. As new properties/characters evolve within a species, the various stages of the evolution of these properties/characters could be assigned a frequency distribution and one could then develop a set-theoretic statement claiming that the frequency of the property in question is different in each stage. Such an approach would appear to be an effective means for tracking character changes within a particular species.

Wilson claims there is much that could be gained from using this set-theoretic approach. "...one could use the formal apparatus of set theory both to model the relations between species and other evolutionary entities and processes...and to examine the validity of inferences made about these matters." (1991, p. 426) Furthermore, the use of set theory to represent species would appear to fit well with the aim to axiomatize at least parts of evolutionary theory.[24]

Although the use of a set view of species seems merely a logical exercise, advocates of Process Structuralism appear to utilize a set view of species more effectively in their aim to develop general laws about species. It might well be that a neo-Darwinian

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[24] Such an approach might fit well with a positivist notion of scientific theories. However, the question, as we saw near the end of Section II in this chapter, is whether the generalizations developed about species would be sufficiently lawlike.

approach to species is less conducive to a viewing species as sets than a Process Structuralist approach. We will examine this more closely below.

Objections to the Proposed Set View of Species

In response to Kitcher's original arguments, Sober (1984a) expresses concern about viewing species as sets. First, he suggests that Kitcher's use of the fallacy of incomplete translation changes the subject. Although he admits the use of set-theory is possible when viewing species, he sees the attempt at doing so as merely a creative exercise. Furthermore he argues that viewing species as sets leaves one unable to *nonarbitrarily* chose between various levels of biological entities when constructing a species set. Sober questions, "why should we identify them [species] with sets of *organisms*, rather than with sets of *local populations, families, generations,* or *cells*?" (1984a, p. 338) Clever translation should allow one to conceive of species as sets of any one of these types of entities. Since there appears to be no biologically legitimate way of choosing between these levels, Sober concludes that species ought not be viewed as sets after all.

It would appear that Sober attempts to take an apparent benefit of the set-theoretic approach and turn it into a problem. But, it is not clear why viewing species at various different levels of specificity is such a problem. Clever translations which allow biologists to view species as sets in a number alternative ways could possibly be of significant benefit to biology. Tracking changes in set membership for a number of different types of sets pertaining to a given species might yield important biological data concerning rates of evolution among species or the level at which selection is occurring in a species. Furthermore, since local populations are made up of families, and families are made up of organisms, and organisms are made up of cells, and on down the line, it apparently would not matter any great deal which of these levels we chose to view a species as a set. Such a decision might reasonably be made on pragmatic grounds; those interested in macroevolutionary phenomena might identify a species with a set of populations or families, those interested in microevolutionary phenomena might identify a species with a set of organisms or genes. However, this would not mean the information gathered from a set of populations would be different, in principle, from information gathered from a set of organisms. The information is merely occurring at a different level of description. All the various ways of viewing species as sets that Sober mentions would appear to fit under the neo-Darwinian framework. Although species appear to act more like individuals, it would seem that Sober attempts to close the door prematurely on a set view of species.

So, it seems species might fruitfully be viewed as sets of entities. However, as it stands, such an approach appears to come with a heavy price. By distancing themselves from essentialism and classes, advocates of a set-theoretic view of species (i.e. Kitcher and Wilson) may have actually conceded the ontological debate. This is because a set view of species seems merely to leave us with the conclusion that species can be represented as sets rather than the stronger conclusion that species are actually sets. Interestingly, Kitcher (1987, 1989) even suggests that the ontology of species is *biologically neutral* in the sense that whether we decide to view species as sets or as individuals does not depend on the biological situation at hand.[25] This view is also

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[25] Kitcher's view seems slightly overstated in light of his parthenogenic lizards example, which we will examine shortly, since it would be hard to call a set of historically disconnected organisms an individual in any meaningful sense of the term.

mirrored in a suggestion made by Wilson who merely aims to consider "whether species can be conceived of as sets, and, if so, whether there is any utility in doing so" (Wilson 1991, pp. 414) as opposed to being concerned with the truth of the matter of species ontology. All in all, unless advocates of a set view can show that evolutionary theory contains situations where viewing species *ontologically* as sets has some positive value, the mere fact that Kitcher and Wilson have shown that species can be *represented* as sets does not seem to seriously undermine the Evolutionary Term argument.

Kitcher's Parthenogenic Lizards Counterexample

Kitcher (1984a, 1989) believes he has found a number of evolutionary situations that require evolutionary biologists to view species as sets.[26] He offers a rather interesting counterexample to the Evolutionary Term argument involving two identical hybrid populations of parthenogenic lizards branching off from the same parental species at different times. Kitcher aims to show that "there are cases in which it would be proper to admit a historically disconnected set as a species." (1984a, p. 314) Kitcher holds that individuality requires historical connectedness among the parts. He reasons that any situation where it would be proper to admit a historically disconnected set of organisms as a species is evidence against the wholesale acceptance of the Evolutionary Term argument. Such a historically disconnected species would seem to require identification via some shared property or trait. Kitcher's proposed counterexample involves a hybrid

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[26] It is worth noting that if biological situations exist where historically disconnected organisms ought to be named as a species, then it seems Kitcher's neutrality thesis is suspect. Kitcher apparently missed the apparent conflict between holding, on the one hand, that the ontology of species is biologically neutral and holding, on the other hand, that some biological situations require species to be viewed as sets.

parthenogenic lizard species, *Cnemidophorus tesselatus*, which he claims could all too easily have been historically disconnected.[27]

Kitcher invites us to imagine two scenarios in which historical disconnectedness among the organisms in *C. tesselatus* could arise. In the first scenario, suppose that two lizard species interbreed at time t_n, produce a hybrid parthenogenic population of *C. tesselatus*, and then at time t_{n+1} *C. tesselatus* goes extinct for some reason.[28] Furthermore, suppose that at time t_{n+2}, the same two lizard species interbreed yet again and produce another hybrid parthenogenic lizard population which falls within the same ecological setting as the previously named *C. tesselatus*, has the same genetic structure as the previously named *C. tesselatus*, and has the same behavioral and morphological characteristics as the previously named *C. tesselatus*. Kitcher claims *there is no biological purpose to be served* by calling these two different hybrid lizard populations separate species. His reasons seem clear and convincing; every interesting biological aspect of both populations is the same.

Kitcher offers a second scenario of how historical disconnectedness among *C. tesselatus* could occur; suppose the first population of *C. tesselatus* produced at t_n did not go extinct at t_{n+1}. In this second scenario, both hybrid populations that were produced at t_n and t_{n+1} respectively would exist concurrently, but they would be considered

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[27] Parthenogenic organisms are capable of self-fertilization. *C. tesselatus* consists mainly of females that are self-reproducing.

[28] Walker et al (1997) suggest that the hybrid species *C. tesselatus* resulted from intebreeding between *C. tigris* and *C. gularis*. Interestingly, an organism from *C. tesselatus* is later assumed to have interbreed with an organism from *C. sexlineatus* to produce another hybrid parthenogenic species *C. negostrics*. What makes *C. negostrics* so interesting is that the organisms in this species are triploid instead of diploid. This fact about *C. negostrics* is good reason for saying that *C. negostrics* is a distinct species since its triploid nature makes introgression between itself and the parental species unlikely.

historically disconnected since they have different origins. Kitcher again claims that in this second case *no biological purpose is served* by calling each of the concurrent hybrid lizard populations separate species. He concludes his presentation of the two scenarios by saying, ".....it is not necessary, and it may not even be true, that all species are historically connected." (Kitcher 1984a, p. 315) If Kitcher is correct about these scenarios, then it would appear that a set view would need to be employed when identifying the species in the scenarios.

Sober (1984a) criticizes Kitcher's presentation of the hybrid lizard case. He suggests that Kitcher does not really understand what the species-as-individuals thesis entails in such a situation. Sober argues the individuality thesis (i.e. the Evolutionary Term argument in particular) does not require biologists to match species up with single origination events. Again he appeals to Mayr's founder principle for support. Sober says,

> "An individual may have parts that had their separate origins; a fleet of ships may have its component boats constructed in different ship yards. Indeed, there is nothing in the founder principle that requires that the founder population [of a species] be a single parental unit." (1984a, p. 340)

Sober's point appears to be that the proper perspective needs to be maintained when assessing the origin of a species. When viewed up close, any species might appear to have multiple origins. However, when viewed from a greater distance, say at the populational level, species appear to have a single origin. Not every single budding phenomena on a branch need be considered as if it were the origination of a new species individual. Recall from Chapter 2 that Sober holds whether such buddings are considered to be separate individuals (i.e. species) depends on what happens later. Phylogenetic relations and species individuation are to be determined retrospectively.

Kitcher suggests that Sober's reply ends up conceding that species can be historically disconnected, since Sober admits that the founder principle does not restrict the origin of a species to one parental unit. There is something important about Kitcher's suggestion. To see why, recall that Kitcher's counterexample involves the production of a hybrid parthenogenic (i.e. self-fertilizing) lizard population; the means of reproduction are contained within each individual organism in this population. However, not all cases of hybridization result in the production of self-fertilizing species. Hybrid species that produce sexually would *a priori* be historically disconnected in some sense, since without a conspecific, a singly produced sexual hybrid organism that is reproductively isolated from its parents would perish without reproducing. This suggests that all sexually reproducing species that are a product of hybrization will be historically disconnected in the early stages of their formation. Although this specific sense of historical disconnectedness among sexual hybrids is not directly discussed by Kitcher, it is similar to what Kitcher believes Sober implicitly admits to by defending the Evolutionary Term argument with the founder principle.

Although Kitcher's response is technically correct, an admittedly more interesting sense of historical disconnectedness exhibited by a species would involve having disconnected parts or members for a significant portion of the existence of a species. Kitcher (1989) suggests that occasionally populations in a species become separated from each other for a period of time and yet reconvene later to continue interbreeding.

Examples of such disconnectedness might arise whenever a temporary geographical barrier divides a species for a number of years.

Ereshefsky (1991) also argues that species can consist of historically disconnected populations. He cites Erlich and Raven (1969) and other biologists who hold that populations within a species may not have any gene flow between them. Ereshefsky does go on to suggest, however, that such species are not historically disconnected overall, since such species have a single origin which is easily recognizable.

We might distinguish then, between degrees of historical disconnectedness. On the one hand, a species might start out historically connected, become disconnected, and then later reconvene. This we can identify as *temporary historical disconnectedness*. Also, there are occasions when a species starts out historically connected, but then becomes disconnected over time and does not reconvene. This we can identify as *later stage historical disconnectedness*. It seems clear that Kitcher's lizard counterexample is strongest if it supports the idea that species can consist of populations that are historically disconnected throughout the entire existence of at least two of the involved populations. We can identify such a case as involving *overall historical disconnectedness*. In the second scenario of his lizard counterexample Kitcher suggests it is possible that the two hybrid populations of *C. tesselatus* will not eventually join together but will proceed onward into the future as two historically disconnected populations that never interbreed. This would be a clear case of overall historical disconnectedness. What ought we say in the case of such an occurrence? Are these two populations the same species or different?

As with most dilemmas, there are advantages and disadvantages to either answer in this case. Furthermore, the nature of these advantages and disadvantages are largely determined by the theoretical background of those attempting to answer the dilemma. Advocates of the Evolutionary Term argument seem to face the following dilemma. On the one hand, if they recognize just a single species in Kitcher's second scenario, then they appear to admit that some species can be historically disconnected throughout their entire existence and, in turn, would need to admit that not all species need to be individuals. On the other hand, if advocates of the Evolutionary Term argument continue to embrace the idea that evolutionary processes require species to be individuals and, in turn, recognize two separate species in Kitcher's second scenario, then they appear to admit that the concept 'species' fails to countenance a significant evolutionary event, namely the apparent production of biologically identical organisms at historically separate times.

Neo-Darwinians appear to have at least two reasons in favor of distinguishing two different species in Kitcher's second scenario. First, the vast majority (if not all) of the species *currently* recognized by neo-Darwinians fit with the species-as-individuals thesis. Neo-Darwinians suggest that the situation described in Kitcher's second scenario is merely a hypothetical example that does not represent the majority of grouping phenomena in the biological world. Second, even if the situation decsribed in Kitcher's second scenario were to occur reguarly, neo-Darwinians such as Ghiselin appear content with letting such situations go unrecognized as species if the situations pose problems for an existing ontological view that works reasonably well.

Recall from Chapter 2 that Ghiselin argues against recognizing groups of asexual organisms as species since such groups fail to meet the definition of species as provided by the biological species concept. Although we are now considering the ontological problem instead of the biological problem, it seems that neo-Darwinians, like Sober, offer a Ghiselin-type argument when considering whether to recognize situations like the one laid out in Kitcher's second scenario. Even though the scenario laid out by Kitcher is interesting from an evolutionary standpoint, neo-Darwinians appear content to hold firm in their denial that there is only one species by claiming that not every interesting evolutionary event needs to be captured by the concept 'species.'

However, one might plausibly argue that contemporary evolutionary biologists ought not distinguish two species in Kitcher's second scenario. It seems that by distinguishing two species in Kitcher's second scenario, neo-Darwinians fail to consider relevant biological events when deciding what ought to count as a species. This line of argument bears some similarity with Kitcher's (*) principle. Recall that Kitcher's (*) principle holds that a proposal to call the parts of a lineage a species should only depend on the properties and relations *intrinsic to the parts in the lineage in question* and not on the properties and relations of parts of other lineages (future, concurrent, or past). What Kitcher sees as most important to species determination is the actual biology occurring within the the lineage in question at the time of determination. In a sense, a similar point is made when Process Structuralists claim that the biology intrinsic to both lineages in Kitcher's counterexample ought to dictate whether we identify two species or one, instead of allowing the preferred ontological outlook to dictate our species identifications. Neo-Darwinians refuse to acknowledge just one species in the Kitcher's second scenario because of their commitment to the ontological view of species. But it seems a bit suspect to fail to even consider the possibility that a species might exhibit overall historical disconnectedness just because we want to preserve a particular ontological view of species.

Non-Darwinians such as advocates of Process Structuralism believe there is good cause to distinguish just one species in Kitcher's second scenario. Recall that Process Structuralists believe the primary causal factor of species are morphogenetic or transformational fields which dictate the development of the organisms in these fields. Recall also that genealogical relations are merely used to explain minor variations among organisms within these fields. As a result, it is quite possible, and even quite likely in many cases, that species picked out by Process Structuralists will be polyphyletic from a genealogical point of view. Remember that a polyphyletic taxon is one which includes organisms from more than one ancestor. From an ontological point of view, polyphyletic taxa must be understood as sets. It makes little sense to attempt to refer to a polyphyletic taxon as if it were a single individual. Such an attempt seriously stretches the meaning of the word 'individual.' Advocates of Process Structuralism would have no trouble accepting that the two lizard populations in Kitcher's second scenario are one and the same species. According to the Process Structuralist account, the lizard populations appear to form a polyphyletic taxon which is governed by the same transformational field.

The Process Structuralist account appears to embrace a particular biological phenomenon in the Kitcher scenario that neo-Darwinians are content to ignore. In essence, the neo-Darwinian approach to such Kitcherian scenarios is reminiscent of the approach used by advocates of the phylogenetic species concept when faced with a branching event. According to advocates of the phylogenetic species concept, the concept of strict monophyly dictates that the ancestral species does not survive a branching event. This has the appearance of putting a theoretical criterion ahead of a certain biological phenomenon when making species identifications. Neo-Darwinians appear to similarly prioritize a theoretical criterion over certain biological phenomena in Kitcher's second scenario.

So it would appear that the acceptability of the main premise of the Evolutionary Term argument depends in large part on the theoretical background of the biologists who are making the species determinations. Neo-Darwinians would appear to be committed to the idea that evolutionary theory requires species to be understood ontologically as if they were individuals. Non-Darwinians such as the Process Structuralists would appear committed to the idea that species are best understood as if they were sets of organisms. Both approaches seem reluctant to examine what the opposing approach feels is biologically relevant phenomena when making species determinations. On the one hand, neo-Darwinians fail to admit that a species can exhibit overall historical disconnectedness. On the other hand, non-Darwinians such as the Process Structuralists fail to see the importance of waiting to see what happens in the future when making species determinations. The question this difference in ontological outlook leaves us with is whether both accounts can be incorporated into a single account of species pluralism.

We will examine in the next chapter whether a legitimate account of species pluralism can be offered that embraces both a neo-Darwinian and a non-Darwinian (a la Process Structuralism) approach to species. We will now turn to examine a different critique of the species-as-individuals thesis. Both the No General Laws argument and the

Evolutionary Term argument presuppose there are only two ontological categories to choose from, namely species can only be classes (i.e. sets) or individuals. We will now examine some critiques of this presupposition.

IV. Weakened Versions of the Species-as-individuals Thesis

There is no question that the species-as-individuals thesis has had a significant impact on our current understanding of the evolutionary process and the associated taxa that partake in that process. Although the species-as-individuals thesis is closely associated with neo-Darwinian theory, there are some neo-Darwinians that are uncomfortable with the limited ontological categories offered in the major arguments for the thesis. These neo-Darwinians do not outright reject the species-as-individuals thesis, however they feel the ontological notion of 'individual' does not correctly apply to the biological notion of 'species.' They advocate weakened versions of the species-as-individuals thesis in order to better capture the ontological nature of species. In a sense, they offer a slightly modified version of the Evolutionary Term argument which concludes that species are something like historical entities instead of individuals. Consideration of these weakened versions of the species-as-individuals thesis is important because, given that one of these weakened versions is deemed legitimate, the job of developing an account of species pluralism that incorporates a wide range of biological interests while still being theoretically consistent might be made easier.

Mishler and Brandon: Aspects of Individuality

Mishler and Brandon (1987) present an alternative account of the notion of individuality within evolutionary biology. They do so in the hopes of making better sense of how it is that species can actually be labeled as individuals. They believe that most of the species recognized by practicing evolutionary biologists fail to meet the definition of individual as defined by Hull and Ghiselin. So, rather than trying to force species into a rather inflexible notion of individuality, Mishler and Brandon weaken the species-as-individuals thesis so that it fits better with the contemporary way in which evolutionary biologists identify species.

Mishler and Brandon begin by suggesting that the class-individual distinction is too simple. They are partial to the species-as-individuals thesis but they argue this thesis is problematic because it glosses over four separately important aspects of individuality. Their main aim "is to argue against the largely tacit assumption that entities meeting some of these criteria [of individuality] will meet them all." (1987, p. 398) Mishler and Brandon strongly oppose the view that species are classes on the grounds that it is not *productive*, but they feel the individuality thesis is not quite correct either.[29] They claim within evolutionary biology there are four separate aspects of individuality that various species taxa possess. More importantly, they claim that not every aspect of individuality is possessed by every species taxon. In light of this, instead of throwing out the species-as-individuals thesis, Mishler and Brandon hold a weakened version of the thesis: *species taxa are best understood as individuals insofar as every species taxon exhibits at least one of four aspects of individuality.*

The four aspects of individuality they pick out are; (1) spatial restrictedness, (2) temporal restrictedness, (3) integration among parts, and (4) cohesion among parts. The first two aspects refer to patterns which result from biological (more precisely,

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[29] Actually, they admit that a "set view" of species is possible, but they reject it because they believe it is unproductive.

evolutionary) processes. The last two aspects refer to causal processes that produce integration or cohesion. They note that cohesion among parts is a necessary condition for integration among parts but the contrary is not true.

It is their contention that for the most part, the groups of organisms labeled as species *do not* exhibit all four aspects of individuality. Furthermore, they hold that species individuality is often dependent on a given process and a species individuation based on one process may not be available in a different situation. For example, although gene flow may work well in some instances, gene flow is not always apparent within groupings that nonetheless show a sufficient degree of integration.[30]

It is important to get clear about what Mishler and Brandon mean when they refer to these four aspects. Consider first the notion of spatial localization. Basically, to say that a species taxon is *spatially localized* means that the species taxon is spatially localized to a particular environment and all its parts occur within this same environment. This aspect helps differentiate between abstract things like classes from particular things like individuals. Classes do not have a spatial location; individuals do.[31]

By *temporal restrictedness*, Mishler and Brandon mean having a single beginning and potentially having a single ending. It follows from this definition that temporally restricted species taxa may not re-originate. By re-originate Mishler and Brandon mean something like coming back into existence after being out of existence for some time.

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[30] Recall from Chapter 2 the phylogenetic species concept offered by Mishler and Brandon which makes available various causal "ranking" criteria for species labeling.

[31] Certainly more might be said about the difference between abstractness and particularity. However, our intuitive notion of this difference seems sufficient for our purposes. For a rather in depth analysis of abstractness and particularity (as well as related notions) see Ghiselin (1997).

Once a species taxon goes extinct, it cannot be reformed. This aspect echoes Hull's infamous phrase, "to be a horse one must be born of horse." (Hull 1978, p. 349)

Integration among parts and *cohesion among parts* are somewhat similar notions but they differ in at least one important way. Mishler and Brandon suggest that integration among parts refers to direct *causal* interaction among the parts of a species taxon. Gene flow is the most common evolutionary process that causes integration; density-dependent natural selection is another. Cohesion among parts is a little weaker notion. They suggest that cohesion refers to uniform behavior as a whole in response to some process without complete or direct causal interaction among the parts. In order to get a better understanding of this aspect it might help to imagine some cherries suspended in a bowl of gelatin. Although all the cherries move uniformly as the bowl is moved around, there is no causal interaction among the cherries. Cohesion can result from a number of processes such as developmental canalization, homeostatic constraint, and density-independent natural selection.[32]

Mishler and Brandon mention that depending on how 'species' is defined, temporal restrictedness might be viewed as decoupleable from spatial localization; that is, a species might be said by some to be spatially localized without being temporally restricted. An example they offer as a potential possibility of this is the case of repeated polyploid speciation in plants via hybridization. Recall from Chapter 2 that polyploid speciation via hybridization occurs when organisms which typically do not interbreed and which possess a different number of chromosomes end up interbreeding and producing

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[32] Mishler and Brandon refer the reader to Holsinger (1984) for a description of these and other important processes. Ridley (1996) is another source.

offspring with an odd number of chromosomes. Such an occurrence would mean that the offspring is effectively cut off from interbreeding with any of the parents or the parent's peers; no backcrossing (e.g. introgression) is possible. Hence, instantaneous speciation is taken to have occurred in such cases. Mishler and Brandon suggest that some biologists might believe it is possible for the same type of polyploidy event to occur on a number of occasions so that a species may turn out to have a certain spatial location while still exhibiting temporal unrestrictedness because of the numerous origination events that brought the polyploid species into existence.

Although they raise this possibility mainly for philosophical reasons, Mishler and Brandon do not appear to suggest such a polyploid grouping ought to be considered a species. This is because such a polyploid species would violate the strict monophyly criterion of their phylogenetic species concept. Recall that the definition of strict monophyly which Mishler and Brandon accept for the purposes of grouping organisms into species holds that all and only descendants of a common ancestor be included in a species. In light of this, it would appear that whenever a newly created polyploid species has more than one polyploid origination event, it is not possible for the monophyly criterion to be met. Grouping repeated instances of the production of a polyploid organism from multiple pairs of hybrid parents into one species taxon would require Mishler and Brandon to countenance a host of species groupings that violate their monophyly criterion.[33] If, as Mishler and Brandon claim, species are to be

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[33] As we have seen already, Kitcher's example of the parthenogenic lizards would be one such species grouping.

monophyletic, it seems that species taxa must meet both pattern criteria; species must be spatially *and* temporally restricted.

We have already examined Mishler and Brandon's claims about the plurality of causal processes that might be used to individuate species taxa in Chapter 2. Their distinction between integrating forces and cohesive forces helps make their reasons for accepting a pluralism of causal processes more clear. Not all genealogical groupings worthy of being called species meet the criterion of integration. Some species taxa are merely cohesive. Recall from Chapter 2 that Erlich and Raven (1969) argue most species are not integrated by gene flow. Instead, they suggest most species derive their cohesion from selective forces or homeostatic mechanisms which constrain the types of mutations that arise.

Kluge on Contemporary and Historical Individuals

Following upon Mishler and Brandon's account of individuality, and one offered by Wiley (1981), Kluge (1990) offers another weakened version of the individuality thesis. Although he rejects the phylogenetic species concept developed by Mishler and Brandon, he accepts the basic account of individuality they give. However, instead of saying that species have *aspects of individuality*, he distinguishes between two different types of individuals. According to Kluge there are *contemporary* individuals and *historical* individuals. Contemporary individuals are those entities that meet *all* the criteria given by Mishler and Brandon. Contemporary individuals are spatiotemporally connected and they have some sort of cohesion and integration. Historical individuals, on the other hand, are those entities that merely meet the pattern criteria given by Mishler and Brandon. That is, such entities are merely spatiotemporally connected; there is neither cohesion nor integration among their parts. Kluge points out that Wiley (1981) referred to more inclusive (i.e. higher) taxa as "historical groups" since such groups merely meet the pattern criteria, and he goes on to say that a strong case could be made for treating species as merely historical individuals. His reason for this stems from his belief that only the parts of species play direct roles in the evolutionary process; species *as whole units* do not play a role in the evolutionary process. Kluge's reasoning certainly appears correct if we take a temporal approach to species identification. It would be hard to claim that all the parts of a species are subject to the same evolutionary forces over a long period of time.

Historical Entities versus Individuals

These weakened versions of the species-as-individuals thesis raise a serious question about the arguments offered in favor of the species-as-individuals thesis. In their basic forms, the arguments presuppose a strict dichotomy between individuals and classes. For example, in an extremely abstract form, the Evolutionary Term argument looks something like the following; "Either species are individuals or they are classes. Species cannot be classes. Hence they must be individuals." However, as the weakened versions of the species-as-individuals thesis seem to indicate, the choice to refer to species as 'individuals' often seems a bit off the mark. To put the problem in a simple form, species do not appear to be individuals in the same sense that human organisms are individuals.

If we reflect on the weakened versions of the species-as-individuals thesis, it seems that its advocates are suggesting that evolutionary theory requires the parts of species at least be *historically connected* by a parental pattern of ancestry and descent.

This means that not all species will necessarily exhibit integration. However, this sense of species might be more defensible. Whether species are actually individuals in the regular sense of that they exhibit integration is not really that important. The important question is whether or not evolutionary theory requires species to be historically connected by ancestor-descendent relations. To capture this reformulation of the species-as-individuals thesis, we might say that the weakened versions of the species-as-individuals thesis aim to conclude that species are *historical entities*.

Ontology versus Practicality

The debate over whether species are individuals or historical entities leads into another debate concerning the strength of the conclusion drawn by advocates of the species-as-individuals thesis. When advocates present their arguments it would appear that they attempt to conclude that species are *actually* individuals or historical entities. Recall, however, that many of the objections to the species-as-individuals thesis hold that species can be viewed as sets. It would appear possible then to be an advocate of the species-as-individuals thesis merely on instrumental grounds. Such an instrumental approach would allow one to merely hold that evolutionary theory requires biologists to view the groups of organisms we identify as particular species *as if they were* individuals or historical entities but not really believe that species actually are individuals or historical entities. Advocates of such an instrumental approach would suggest evolutionary biologists ought to remain agnostic about the ontological status of the groups of organisms we identify as particular species.

Wilson (1991) addresses this difference between actuality and instrumentality in the following way. He suggests there are two different concerns regarding the ontology of species; first, in a metaphysical sense, there is a concern about whether species *really* are individuals, classes, or historical entities. However, in a second sense, there is a concern about whether it is *possible* to view species as individuals, classes, or historical entities. Although the groups of organisms we identify as particular species might really be classes, we might still hold that it is beneficial to view these various groups of organisms as if they were individuals or historical entities. Of course the opposite might be true as well; although the groups of organisms we identify as particular species might really be individuals or historical entities, we might still hold that it is beneficial to view these various groups of organisms as if they were individuals or historical entities. Wilson suggests much of the debate over the ontology of species within evolutionary biology revolves around the second concern.

Rosenberg (1985, Chapter 7, Section 6) embraces a view that is consistent with Wilson's take on the ontological problem. Rosenberg suggests that the point of contention between proponents and opponents of the species-as-individuals thesis is whether the organisms of species can be arranged into biologically interesting classes. He argues that although species do not *logically* have to be individuals, the species-as-individuals thesis should not be taken as advocating something that strong. Rather he offers a version of the No Lawlike Generalizations argument by suggesting that biologists ought to embrace the species-as-individuals thesis because it is the best explanation of the fact that biologists cannot find any properties in common among organisms in a species.[34]

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[34] Sober (1984) seems to suggest something similar when he says that the individuality approach is the most promising in systematics. See also Hull (1987). It is worth noting that more recently, Wilson (1996) has argued that species are not units of evolution in

Rosenberg does go on to suggest that if the organisms of species can be arranged into biologically interesting *classes*, the species-as-individuals thesis might appear to be in trouble. Rosenberg apparently does not believe it is possible for biology to utilize both a class view of species and an individual view of species at the same time. Ghiselin (1987, 1997) has also voiced opposition to this type of mixing of ontological perspectives within biology.

Although we might find that it is too difficult to answer whether species are actually individuals, classes, or historical entities, there can still be significant disagreement about what ontological framework to utilize when identifying species. We do not escape the ontological species problem by claiming that biologists can never really know the actual ontology of the groups of organisms identified as particular species. Biologists must make a commitment to some type of ontological outlook regarding species, even if this commitment is merely instrumental in spirit.

V. Summary

The two arguments for the species-as-individuals thesis examined in this chapter appear to carry some weight for biologists of a neo-Darwinian persuasion. However, neither argument is conclusive. The No Lawlike Generalizations argument may derive

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any relevant sense since a gradualist interpretation of evolution makes individuation of units impossible and a saltationist interpretation of evolution fails to equate species with units that evolve. Wilson may be guilty of requiring too much from the notion 'unit.' But apart from this, his argument is best understood as an argument against the reality of species and not an argument directly about what evolutionary theory requires from the units in it. As a matter of fact, he argues that populations are really the units that evolution is concerned with. Many advocates of the history-based phylogenetic species concept would seem to agree. In a sense, Wilson's argument might support the claim that species are really just populations which are connected by reproductive links.

much of its force from the fact that biologists have failed to engage in the correct types of inquiry when attempting to uncover lawlike generalizations about particular species. It may well be that further inquiry will lead to the discovery of relatively productive lawlike species generalizations. The Evolutionary Term argument appears to have a bit more force, but Kitcher and Wilson have shown that it is possible to view species a sets in a meaningful way. Also, Kitcher's lizard counterexample raises serious questions about the legitmacy of claiming that every species must exhibit historical connectedness among its parts. Although weakened versions of the species-as-individuals thesis attempt to address the inappropriateness of using 'individual' to refer to species, these weakened versions still stem from a neo-Darwinian point of view; a point of view that ultimately rejects the idea that species are sets. Even these weakened versions of the species-as-individuals thesis still face the difficulties raised by Kitcher's lizard counterexample. Kitcher's lizard counterexample appears to support for those non-Darwinians such as Process Structuralists who appear to be unconvinced by the No Lawlike Generalizations argument and the Evolutionary Term argument. Process Structuralists seem to embrace a set view of all taxa, including the species taxon, because they focus on different biological phenomena than what the advocates of the species-as-individuals thesis focus on.

So it would appear that there is a continuum of ontological positions we might choose from when placing species into an ontological category. We have identified three basic positions; individual, historical entity, and set (or class). It also appears that each ontological position is best suited to particular theoretical interests and biological situations. Consider the following examples. Advocates of the biological species concept identify species that exhibit integration among parts. ‘Individual’ seems an appropriate ontological category for such species. Advocates of the evolutionary species concept and the phylogenetic species concepts need not require integration among the parts of the species they identify. ‘Historical entity’ seems apropos for such species. And finally, Kitcher and the Process Structuralists suggest that structural or developmental processes provide a sufficient foundation for identifying species. ‘Set’ or ‘class’ seem apropos ontological categories for such species.

In light of the different types of species concepts examined in Chapter 2 and the apparent disagreement between neo-Darwinians and non-Darwinians regarding the ontological status of species, it would appear that developing an account of species pluralism which includes all the speceis concepts we have examined faces some interesting theoretical and interdisciplinary challenges. This is because most neo-Darwinians favor the species-as-individuals thesis and in turn accept a systematic taxonomic hierarchy, whereas non-Darwinians like the Process Structuralists favor a set view of species and in turn accept a classificatory taxonomic hierarchy. An account of evolutionary biology that allows for a systematic as well as a classifactory approach to taxonomy would appear to exhibit disciplinary discord. Recall from the Introduction that we briefly defined disciplinary discord as the use of two (or more) inconsistent or possibly incommensurate explanatory accounts to account for phenomena in a given domain.

We will examine some recent accounts of species pluralism in the next chapter in order to assess whether an account of species pluralism can be given that incorporates the theoretical interests of neo-Darwinians as well as non-Darwinians such as the Process

Structuralists. We will first examine a neo-Darwinian account of species pluralism and then move to consider an account of species pluralism that includes both neo-Darwinian and non-Darwinian species concepts. Ulitmately we will find that acceptance of an account of species pluralism will require that some theoretical/disciplinary interests give way. The questions that remain are which ones and how many.

CHAPTER 4: SPECIES PLURALISM

Species pluralism is motivated by there being many different definitions of species in use within evolutionary biology and there being no clear consensus concerning which single definition is best. Ereshefsky (1992, 1995) suggests there are two main approaches philosophers and evolutionary biologists have taken in light of these facts; a rather staunch monistic approach and a pluralistic approach. Species monists believe that one proper definition of species exists and biologists just need to work harder to discover it. Species pluralists believe that the species concept is necessarily heterogeneous, requiring numerous definitions of species to adequately address the complexity of evolutionary biology.

Given the problems each species concept faces, species monism seems fraught with difficulties. As we saw in Chapter 2, there appear to be too many diverse biological situations for a single concept to adequately address. In light of this, some philosophers of biology have suggested that evolutionary biologists ought to accept species pluralism. Species pluralism aims to utilize multiple theories of species simultaneously so as to adequately address every biological situation. Numerous pluralistic approaches have been offered and the debate over species pluralism is rather complicated. We will restrict our examination of species pluralism to two recent accounts; one offered by Ereshefsky (1992, 1995) and another offered by Kitcher (1984a, 1984b, 1989). Both accounts raise interesting philosophical questions about the nature of biology and species because both suggest multiple, incompatible taxonomies arise from species pluralism. Yet an important difference between the accounts is that Ereshefsky's is limited to historically connected species whereas Kitcher's embraces both historically connected and disconnected species. Consideration of their accounts will help us to identify an account of species pluralism that serves a wide array of biological interests, is sufficiently pluralistic, but still refuses to allow just any old species concept. In brief, the aim of this chapter is to examine just how pluralistic an account of species pluralism ought to be.

I. Various Senses of Species Pluralism

Pluralism is used a number of different ways in contemporary biology. In light of this, it is important to get a clear understanding of what *species* pluralism means. Recall from Chapter 2 that Mishler and Brandon claim their phylogenetic species concept is pluralistic. They argue species must be monophyletic but suggest there are a plurality of causal processes that might produce monophyletic groups; processes such as gene flow, homeostatic mechanisms, or selective pressures. The pluralistic nature of their approach to species is not overly controversial, since they do not suggest that pluralism results in the production of multiple, incompatible taxonomies. They claim there is a single correct casual account that ought to be uncovered for each biological situation. They allow for the possibility that more than one causal process can be involved in the production of a species, but they hold firm to the idea that each biological situation has a single, correct causal account. They suggest that the identification of the correct causal story in each situation will lead to the development of a single taxonomic hierarchy.

Ruse (1987) offers a pluralistic approach to species that is similar to Mishler and Brandon's in that he also believes each biological situation has a single, correct causal story that can be used to identify species. He suggests that the choice of which concept to use is determined by the biological situation, yet he believes that each concept ultimately coincides with the others. In a sense, choosing which concept to use really boils down to a matter of convenience, since each concept ultimately identifies the same entities as species as every other concept. Ruse's pluralism also differs from Mishler and Brandon's pluralism, since Ruse does not require evolutionary biologists to employ species definitions that are consistent with the concept of monophyly. However, this last difference is unimportant for our purposes. The important point is that Ruse, and Mishler and Brandon, suggest there is a single correct taxonomy of the world's organic diversity.

We will not consider either of these approaches in our examination of species pluralism for the following reasons. First, both approaches presume that for every biological situation there is a single best species definition that ought to be deployed. Furthermore, both approaches presume that evolutionary biologists all have similar theoretical interests. As we have seen in Chapters 2 and 3, these two presumptions are controversial. Both accounts of species pluralism to be examined in this chapter reject these two presumptions.

Species pluralism, as we will understand the concept, is the position that a given group of organisms can be divided into species groupings by different species concepts, and the species groupings may end up cross-classifying some organisms. Cross classification of organisms occurs when species definition x divides a set of organisms into species $s1_{xsc}$ and $s2_{xsc}$, species definition y divides the same set of organisms into species

$s1_{ysc}$ and $s2_{ysc}$, and the organisms that appear in $s1_{xsc}$ and $s2_{xsc}$ do not match the organisms that appear in $s1_{ysc}$ and $s2_{ysc}$.

Consider the following simple example of how such cross classification might occur. Within a given biological situation, the biological species concept might divide organisms *a*, *b*, *c*, *d*, and *e* into two species; species 1 which consists of organisms *a* and *b* and species 2 which consists of organisms *c*, *d*, and *e*. With regard to that same biological situation, the ecological species concept might divide organisms *a*, *b*, *c*, *d*, and *e* into three species; species 1 which consists of organisms *a* and *e*, species 2 which consists of organisms *b* and *d*, and species 3 which consists solely of organism *c*. In this simple example, the organisms are cross classified by the two species concepts. This cross classification results mainly from the different causal stories that each species concept utilizes to identify species. Cross classification does not always occur when more than one species concept is used in a given biological situation, but the potential for it certainly arises whenever more than one concept is used. It would appear that the potential for cross classification increases according to the number of different species concepts that are utilized in a given biological situation.

We can usefully divide pluralistic approaches that allow for cross-classification of organisms into two main types; those that require species to be historically connected and those that do not. Ereshefsky (1992, 1995) has been the main advocate of a pluralistic approach to species that requires historical connectedness. This stems from his implicit acceptance of the species-as-individuals thesis. Kitcher (1984a, 1984b, 1989), Dupré (1993), and Wilkerson (1993) have offered accounts of species pluralism that do not require historical connectedness. Ereshefsky (1992) has expressed opposition to these less restrictive pluralistic accounts primarily on the grounds that they allow species groupings that are at odds with the neo-Darwinian requirement that species be individuals (or historical entities). He believes that in order for a species concept to be considered legitimate, it must be consistent with neo-Darwinism.

Kitcher argues adamantly in favor of an account which allows for historically disconnected species, as well as historically connected ones, on the grounds that both types of species contribute to a full understanding of the evolutionary process. However, a question that his account needs to face is whether it suffers in any way from tension or discord between the two underlying disciplinary approaches that give rise to both historically connected and historically disconnected types of species concepts. Such tension may ultimately make it difficult to answer the types of scientific questions that lead to meaningful progress. Some biologists suggest that it is possible to integrate both disciplinary approaches into one approach. However, such integration runs the risk of relinquishing any possible benefits of pluralism. We will address the issues of discord and integration in detail after examining Kitcher's account. For now it is sufficient to understand that the apparent tension between the two underlying disciplinary approaches in his account appears linked to the incommensurability of the cognitive activities utilized by the two approaches.

Prima facia Ereshefsky's account does not seem faced with this tension since his account only allows the use of species concepts that result in historically connected species. As we will see, the fact that such species concepts all fall within a neo-

Darwinian framework appears to save Ereshefsky's account from any tension between disciplinary approaches. However, Ereshefsky's pluralism may ultimately be guilty of some of the same sins of species monism, since Ereshefsky only embraces species concepts that are neo-Darwinian in nature. We will address this issue after examining Ereshefsky's account in detail.

So we will focus on determining which account of pluralism is best for biology; Ereshefsky's or Kitcher's. Both accounts appear to have benefits and drawbacks. Ereshefsky's account seems to escape the problem of discord between approaches yet it may not be sufficiently pluralistic. Kitcher's account seems to be more pluralistic yet it may ultimately suffer from discord that prevents meaningful progress. All in all, we will conclude that attempting to integrate both accounts within a Kitcherian account of species pluralism is the most desirable alternative for evolutionary biology, but we will also conclude that the integration must involve concessions from both disciplinary approaches within his account. With this as the backdrop, let us now examine both accounts of species pluralism in detail.

II. Ereshefsky's Species Pluralism

Ereshefsky (1992) offers an account of species pluralism which requires, at the very least, that species are lineages. Basically, a lineage is a series of historically connected ancestor-descendant organisms with a single origin.[1] He also notes that the term 'species' plays two interconnected roles in biology. On the one hand, it plays the

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[1] Ereshefsky views a lineage as a type of individual. Hence, Ereshefsky's lineage requirement reflects his commitment to the species-as-individuals thesis.

role of a basal taxonomic unit within systematics. On the other hand, it plays a role in explaining the diversity of the organic world; 'species' as used by evolutionists, refers to a unit of evolution. Along with Mishler and Brandon, Ereshefsky suggests there are many forces of evolution at work on the organisms that can give rise to different units of evolution. However, in contrast to their position, Ereshefsky claims that attempting to understand how these forces contribute to the world's organic diversity requires multiple incompatible taxonomies that overlap with each other. These multiple taxonomies result from the employment of different species concepts such as the biological species concept, the ecological species concept, the evolutionary species concept, and the phylogenetic species concept, all of which were discussed in Chapter 2.

Ereshefsky offers a quick example to illustrate how the application of different species concepts to a single biological situation can result in taxonomies that cross-classify organisms. He considers the attempt to develop the "correct" taxonomy of insects living on a mountainside. Suppose there are three populations *a*, *b*, and *c*, and that each population is monophyletic, displaying uniquely derived characters. Furthermore, suppose that populations *a* and *b* can interbreed, that populations *b* and *c* share a similar ecological niche, and that population *c* consists of asexual organisms. Each of the three approaches would offer different taxonomies of the insects. The interbreeding approach would say there is a single species consisting of $a + b$. The ecological approach would say there are two species, one consisting of *a* and one consisting of $b + c$. And finally, the phylogenetic approach would say there are three separate species, *a*, *b*, and *c* respectively.

The three taxonomies are incompatible since they end up cross-classifying the same organisms into different species taxa. Ereshefsky notes that this cross-classification can happen in two ways. First, one species may properly contain another species as in the example of the interbreeding species $a + b$ properly containing the phylogenetic species a. Second, an organism may be part of two species that are disjoint as in the example of the organisms in population b in the ecological species $b + c$ and the interbreeding species $a + b$.

Ereshefsky suggests the metaphysics of evolutionary biology provides a reason for preferring species pluralism over species monism. In support of this suggestion he remarks,

> "A taxonomy of monophyletic taxa provides a framework for examining genealogy. A taxonomy of interbreeding units offers a framework for examining the effect of sex on evolution. And a taxonomy of ecological units provides a structure for observing the effect of environmental selection forces. A systematic study that considers just one of these taxonomies provides an overly coarse-grained picture of evolution." (1992, p. 678)

His point is that many evolutionary forces exist (e.g. interbreeding, selection, genetic homeostasis, common descent, developmental canalization) which in turn contribute to the production of discrete and stable groups of organisms. Pluralism provides a more fine-grained picture of the actual evolutionary process that gives rise to species than monism does. Ereshefsky holds that various evolutionary biologists find themselves drawn to study each force respectively. These forces (and their associated evolutionary biologists) can roughly be matched to the various neo-Darwinian species concepts we examined in Chapter 2.[2] Ereshefsky, then, concludes that the metaphysics of evolutionary theory requires species pluralism.

Initial Objections to Ereshefsky's Account

Ereshefsky recognizes that many evolutionary biologists have objections to species pluralism. First, Ereshefsky recognizes that species pluralism is susceptible to the claim that the species concepts he advocates might be reducible to another, more basic species concept; such as a species concept based on genetic similarities. He argues however, that two problems arise for such a proposed reduction. First, he cites evidence from Frost and Hillis (1990) which shows that groupings based on genetic similarity do not always form monophyletic groups, so a genetic species concept will fail to capture a seemingly important aspect of many currently recognized species. Second, he claims that macrolevel (e.g. organismic and populational) incompatibilities among the various taxonomies will arise at the microlevel (e.g. chromosomal and genic) as well, so an attempt to reduce all species concepts to a single genetic species concept will fail to resolve the current problem of incompatibility between species concepts.

Ereshefsky also considers an objection to species pluralism which holds that since pluralism requires the term 'species' to be ambiguous, confusion is bound to set in when

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[2] Ereshefsky only identifies three species concepts in his version of species pluralism. However, the inclusion of more than three species concepts is not inconsistent with Ereshefsky's position. Evolutionary biology may require a few more species concepts to properly account for the various evolutionary processes that contribute to the production of discrete and stable groups of organisms. Ereshefsky's main criterion for inclusion is that a species concept is consistent with the species-as-individuals thesis. Ereshefsky *does* object to the use of species concepts that do not fit with this thesis.

evolutionary biologists discuss the nature of species. He calls this objection the communication objection. Since such confusion is bad for biology, advocates of the communication objection argue that species pluralism should be avoided. Ereshefsky replies to this objection by suggesting that evolutionary biologists drop the general term 'species' and replace it with more precise terms like 'biospecies,' 'ecospecies,' and 'phylospecies.' He suggests that the all encompassing term 'species' is part of an outdated way of thinking about evolutionary theory; 'species' has become much like the term 'phlogiston' or 'immaterial mind'. Ereshefsky reasons that since we now understand there to be many evolutionary forces that contribute to the production of species, we ought to give up our singular use of the term 'species.' Ereshefsky dubs his account of species pluralism "eliminative pluralism" in light of his suggestion that more specific species concept labels replace the all encompassing term 'species.'

In a sense, the communication objection appears to point out a mere practical problem. It is inconvenient and difficult to talk in depth about species with others that use the term 'species' in different ways. Ereshefsky's reply to this objection seems on the right track. Science often requires technical jargon that goes beyond the cursory distinctions drawn by everyday language. Consider for example the common descriptor 'bug.' Such a crude term fails to provide a solid foundation for any scientific inquiry but it serves our everyday purposes quite well.

However, the communication objection also seems indicative of a deeper problem for species pluralism; namely that species pluralism does not provide a consistent view of the evolutionary process. Ereshefsky calls this objection the inconsistency objection.

Recall that a taxonomic hierarchy is a tool that is utilized by evolutionary biologists to organize and explain the diversity of the organic world. Advocates of the inconsistency objection hold that species pluralism allows for different theories of evolution to be lumped together inappropriately. The various taxonomic hierarchies that result from using different theories of evolution allow a mish-mash of taxa that reflect different and inconsistent theories of the evolutionary process. For example, species pluralism allows species taxa from both a cladistic and an evolutionary systematic viewpoint to be represented. Advocates of the inconsistency objection point out that such a mish-mash of species taxa must be represented in different taxonomic hierarchies, *only one of which can be correct.*

Ereshefsky responds to this objection by claiming that although the various approaches to species divide organisms up in inconsistent ways, the approaches all reflect the same tree of life that is based on the actual genealogical record of descent. Each approach to species merely highlights *different aspects* of evolution by dividing up the tree of life in slightly different ways at the point where divergent branching phenomena begin to become visible. Ereshefsky holds that as long as each of the approaches to identifying species accepts that there is a single tree of life based on the actual genealogical record of descent among organisms, then species pluralism does not result in any serious inconsistencies. Even though the various approaches to species will produce their own taxonomies that have different groups as species, the underlying reticulating branching processes of the actual genealogical record of descent will be the same in each taxonomy.

Although Ereshefsky believes he addresses this objection adequately, there might be more to the inconsistency objection than Ereshefsky considers. The inconsistency objection might be pushed a bit farther in the following way. One might object that whenever biologists from different theoretical backgrounds apply their separate species concepts to the organisms in a given situation, there is still a sense in which we are left wondering which of the species concepts correctly identifies the underlying processes for the given situation. The inconsistency that is of concern involves the inconsistent accounts of the notion of an evolutionary unit that species pluralism generates. If species refers to the unit of evolution, then advocates of the monism might say there is a serious sense in which species pluralism results in an inconsistent view of the unit of evolution.

Beatty on Theoretical Pluralism in Biology

Beatty (1997) offers some thoughts about pluralism in general within biology which are relevant to this version of the inconsistency objection. Beatty claims that "theoretical pluralism" occurs throughout all of biology.[3] He distinguishes between two types of "theoretical pluralism." On the one hand, biology is often faced with situations which involve competition, between advocates of various causal agents, to account for the phenomena in a domain.[4] Advocates of each causal account argue that their casual account is *the* primary one. Due to there being insufficient evidence to suggest that one

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[3] His use of the term 'theoretical' in the phrase 'theoretical pluralism' can be a bit confusing. There are levels of theories within science. For example, evolutionary theory contains various "theories" about how speciation occurs. In order to avoid confusion, we will use the phrase 'causal account' to refer to the notion of 'theory' that Beatty has in mind when he discusses "theoretical pluralism."

particular causal account is primary, there are a plurality of causal accounts offered to account for the phenomena in a domain. However, each causal account cannot be correct simultaneously since each cites a causal account that is in conflict with the others. Beatty believes the drift versus selection debate in evolutionary theory is an example of this type of pluralism in contemporary biology.[5]

On the other hand, Beatty suggests contemporary biology also exhibits a slightly different type of pluralism whenever multiple causal accounts are required to cover all the various phenomena in a domain. In such situations, the various biologists who offer their respective casual accounts do not each claim that their account is *the* correct account. Instead, they merely attempt to establish that their respective theory explains a *relatively significant* portion of the phenomena in a domain. The competing causal accounts within a given domain cannot each be true of the phenomena within a domain, yet each account is true of some portion of the domain. In addition, the debate can be one about which account is the most prominent in regards to a single situation. Beatty suggests that within evolutionary biology, a number of relative significance disputes arise because of the contingent nature of evolutionary phenomena. He suggests that no single causal account is offered to explain evolutionary phenomena because such an approach embraces an unacceptably conservative view of evolutionary development. Some examples of relative

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[4] We will discuss the nature of a domain in more detail below. For our purposes here, a domain can be defined simply as the set of phenomena that are being accounted for.

[5] It is not clear that Beatty is right about this debate being a clear example of an and all or nothing debate. It seems that a better example might involve a debate between Creationists and Darwinians.

significance disputes involve disagreement between gradualists and saltationists over the rate of evolution and also disagreement between advocates of the various accounts (e.g. sympatric, parapatric, and allopatric) regarding the speciation process.

The Nature of Ereshefsky's Species Pluralism

Although Beatty provides a good foundation for analyzing pluralism in biology, Ereshefsky's account of species pluralism seems different from both types of theoretical pluralism identified by Beatty. This is in large part because Ereshefsky's species pluralism appears to exhibit characteristics of both types of theoretical pluralism identified by Beatty.

At first glance, the type of "theoretical pluralism" occurring in Ereshefsky's account of species pluralism might appear to involve a type of all or nothing dispute. Advocates of the inconsistency objection hold that if Ereshefsky's account of species pluralism involves the all or nothing type of theoretical pluralism, then it would appear that the inconsistency objection is well founded, since the various species concepts would be in direct conflict with each other. To advocates of the inconsistency objection, it might appear that advocates of the various species concepts in Ereshefsky's account of species pluralism attempt to account for every part of the domain. Hence, the hard-core monist might be duped into thinking that the biologists representing each species concept aim to give *the* correct account of species. Strong evidence in favor of this way of categorizing Ereshefsky's pluralism stems from the fact that the advocates of each species concept have a markedly different understanding of the term 'evolutionary unit.' For example, advocates of the ecological species concept will suggest that the proper unit of evolution is an ecological group maintained by selective forces within the ecological niche, whereas advocates of the biological species concept will suggest that the proper unit of evolution is a reproductive group maintained by the process of interbreeding and isolating mechanisms. Application of one of the species concepts to the domain of apparent discrete and stable organisms divides the domain up in a way that is incompatible with the application of any other species concept. This explains why biologists representing each species concept often end up cross-classifying organisms when their respective taxonomies are compared. Although the advocates of each species concept starts their inquiry with the apparent discrete and stable groups of organisms as a starting point, after all is said and done, each advocate appears to see different units of evolution which are generated by the specific causal process embodied within each species concept. This helps make sense of why different names are needed to refer to the respective species for each advocate.

Although Ereshefsky's account of species pluralism seems to exhibit features of the all or nothing type of pluralism identified by Beatty, Ereshefsky's account appears to be different from this type in some important respects. For example, there seems to be an important difference between the type of pluralism raised by considering whether evolution is caused by drift or selection (which Beatty believes is clearly a type of all or nothing pluralism) versus the pluralism raised by considering how to identify species. The debate between both advocates of selection and drift is an all or nothing debate that requires a pluralistic approach because biologists lack sufficient evidence to determine the primary cause; if there were sufficient evidence, one of the theories would emerge victorious over the other.

Although the unit of evolution refers to a different type of grouping for each species concept in Ereshefsky's account of pluralism, this does not necessarily mean that his pluralism collapses into a type of all or nothing pluralism. Recall that Ereshefsky requires species to be lineages at the very least. This requirement reflects his commitment to an individualist ontology of species. All of the species concepts Ereshefsky embraces accept an historical or genealogical approach to taxonomy. Ereshefsky does not suggest that the advocates of the various species concepts are at odds with each other over larger theoretical issues in the way that selectionists and drift advocates (or Creationists and Darwinians) are at odds. He merely suggests that the idea of there being one type of evolutionary unit should be done away with. The evolutionary process contains various mechanisms and if we are to fully understand this process he suggests we ought to recognize various types of evolutionary units; ecospecies, biospecies, evospecies, phylospecies, etc. Although this is a complicated view of the evolutionary process, as we move up the taxonomic hierarchy and consider more macrolevel taxa, the need for such different names becomes less and less necessary. For example, there does not need to be a distinction between biogenera, ecogenera, or evogenera. The domain, beginning with the taxonomic level genera and proceeding upward, becomes more uniform across the various taxonomies in Ereshefsky's account even if they happen to embrace different ideas about what counts as the basic evolutionary/taxonomic unit. The pluralism, then, in

Ereshefsky's account is a pluralism at a low level in the taxonomic hierarchy, namely at the species level. Pluralism at higher taxonomic levels is not necessary.

So it would appear that Ereshefsky's account escapes the inconsistency objection. In light of this, we might be prompted to conclude that his account of species pluralism involves relative significance disputes. However, his account also seems different from this type of pluralism as well. Recall that the advocates of the various theoretical interests in relative significance disputes do not each aim to account for the entire domain in question; they merely aim to account for a portion of the domain. Ereshefsky's account differs from this because there is a sense in which the advocates of the various species concepts in his account attempt to account for the entire domain. Ereshefsky's insects on the mountainside example is indicative of this. Each species concept involved in that example divided up the parts of the domain in question in its own way. The aim for advocates of each species concept is to account for as many insects as possible. Of course the interbreeding approach fails to recognize groups of asexual organisms, but its advocates defend this non-recognition by suggesting that such groupings are a small, unimportant percentage of the overall set of grouping phenomena. Mishler and Brandon's account of species pluralism would appear to be more representative of a species pluralism that involves relative significance disputes. Recall that they suggest there is a single best species concept that applies to each biological situation.

In light of Ereshefsky's pluralism not fitting neatly into either type of pluralism identified by Beatty, we might distinguish a third type of pluralism in between Beatty's types to better capture the pluralistic sense of Ereshefsky's account. According to

Ereshefsky's account, there will need to be multiple causal accounts cited in order to get a full picture of evolution. However, these multiple causal accounts do not work together like an environmental causal account and genetic causal account might augment each other to provide an overall picture of what caused a final organismal product in a certain case. Citing both environmental and genetic causes to account for why an organism looks the way it does implicitly suggests that advocates of both causes are dealing with the same domain. However, the advocates of the various species concepts are not really dealing with the same domain. This is reflected in the fact that the various advocates of species concepts end up identifying 'ecospecies,' 'biospecies,' or 'evospecies,' etc. In effect, each species name refers to a different type of entity. However, the degree of conflict between the theoretical interests in Ereshefsky's account is much less than what occurs in all or nothing disputes. Ereshefsky holds that the only legitimate species concepts are those that view species as lineages (or historical entities). In effect, Ereshefsky requires species concepts to be consistent with neo-Darwinian theory. As a result, although the various theories of species all pursue separate interests, each is part of a larger, all encompassing theory.

Ereshefsky's attempt to limit the acceptable species concepts to those consistent with neo-Darwinism raises some important questions. Is he committed to a certain type of monism? (It would apparently be monism at a higher theoretical level than the species level.) If so, what ramifications does this have regarding the potential for progress in science? Does his account of species pluralism include enough diverse theoretical interests in order to do biology properly? Ereshefsky believes limiting the species concepts to those consistent with neo-Darwinism allows him to adequately address another objection to species pluralism called the anything goes objection. This objection holds that species pluralism is dangerous since it will invariably allow all sorts of illegitimate species concepts (e.g. a creationist species concept) to be considered on par with legitimate ones. However, there is a fine line between adding too much and taking away too much. Beatty suggests that an important benefit of a pluralistic approach is that it pushes the envelope of science and encourages progress. Ereshefsky's account might be too limited to properly push the envelope of biology and to properly investigate all biological phenomena. We will examine Ereshefsky's response to the anything goes objection below, but first we will consider a more inclusive account of species pluralism; one that might do a better job of pushing this envelope, but one that may ultimately suffer from discord due to the inclusion of widely different disciplinary approaches.

III. Kitcher's Account of Species Pluralism

Kitcher (1984a) offers a version of species pluralism that recognizes historically *disconnected* species as well as historically connected ones. Kitcher's motivation for species pluralism is somewhat similar to Ereshefsky's, but there is an important difference as well. Kitcher (1984a) claims that because of the underlying biological complexity, one particular species concept is unable to serve all the diverse interests of biologists. Although the various species concepts may each account for an important grouping pattern in the organic world, each species concept alone is unable to account for every important grouping pattern. The biological species concept, for example, picks out groups of organisms that interbreed in reproductive isolation. Recall that Mayr's mosquito example discussed in Chapter 2 focuses on such grouping patterns. However, as we have seen, other grouping patterns based on ecological resources or selective forces exist.

There is a subtle, but important, difference in motivation between Kitcher and Ereshefsky regarding why species pluralism is necessary. Ereshefsky suggests that each species concept covers the domain of apparent discrete and stable groups of organisms fairly completely. He suggests a pluralistic approach because he believes that utilizing many different species concepts will provide us with a better understanding of the evolutionary process. Kitcher appears to have a slightly different motivation for species pluralism. He holds that each species concept fails to adequately account for the full domain of apparent discrete and stable groups of organisms. He suggests a pluralistic approach because there are so many apparently legitimate discrete and stable groups of organisms that one species concept cannot possibly serve all the interests of biology. Kitcher even suggests that the species concepts used by biologists need not be neo-Darwinian. As we will see, an important question facing Kitcher is whether all the species concepts he recognizes reflect a legitimate biological causal process/structure.

Borrowing from a distinction made by Mayr (1961), Kitcher suggests there are two main, equally legitimate, explanatory projects in biology; structural and historical. He claims each project provides a foundation for various species classifications. The projects are derived from the two main fields of biology identified by Mayr; functional and evolutionary. According to Mayr, functional biologists pursue "how" questions, for example, questions concerning how the human heart functions or how the human immune system functions. Evolutionary biologists on the other hand pursue "why" questions, for example, questions concerning why humans have hearts or why humans have immune systems. Mayr goes on to suggest that the relationship between functional and evolutionary questions is as follows; functional questions aim to identify more immediate, proximate causes for observed phenomena whereas evolutionary causes are more distant, ultimate causes. Although he notes that both types of causes need to be accounted for in order to achieve a full understanding of biological phenomena, his association of proximate cause with functional questions and ultimate cause with evolutionary questions seems to imply that only evolutionary questions get at the heart of the causal matter.

Mayr's suggestion that evolutionary questions aim to identify ultimate causes might be a bit odd for two reasons. First, as we saw in Chapter 3, most neo-Darwinian explanations of species will involve the use of narratives instead of the use of lawlike generalizations. Second, only the answers to "why" questions are traditionally viewed as providing ultimate explanations, since answers to "why" questions have traditionally been derived from some lawlike generalization. Together, these two reasons might suggest the idea that evolutionary questions merely aim at identifying proximate causes.[6]

But it is important to note that the issue under consideration here is not whether answers to evolutionary questions *explain*; they may well do this in some way. Hull

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[6] This albeit brief analysis may help explain the motivation behind the No Lawlike Generalizations argument in Chapter 3. "Why" questions about particular evolutionary species are not easily answered since, if species are individuals, then biologists ought best be pursuing descriptive "how" questions about them instead of looking to uncover lawlike generalizations about them.

(1975) suggests that the explanatory power of a narrative might well be as valuable as a derivation of some phenomena underneath some law. He compares the explanatory value of a narrative to the satisfaction derived from holding all the parts of a novel or symphony in their proper place in one's mind. He ultimately believes that such narrative explanations are of equal value to the types of explanations derived from subsuming particulars underneath lawlike generalizations. Hull's position is certainly one that would help make sense of Mayr's claim about evolutionary questions aiming to provide ultimate causes.[7]

Following Mayr's lead then, Kitcher suggests there are two main explanatory projects within contemporary biology; structural projects and historical projects. Kitcher suggests that structural explanatory projects seek to explain things like morphology, developmental processes, or functions of organs amongst similar organisms. Historical explanatory projects seek to explain facts about the *genealogy* and *evolution* of morphology, developmental processes, or functions of organisms.

However, Kitcher deviates from Mayr's analysis of the two types of projects by suggesting that neither project is more fundamental than the other. Kitcher claims that knowing the answer to questions posed in a structural inquiry does not provide answers to questions posed in an historical inquiry, nor vice versa. Whereas for Mayr, evolutionary causes are ultimate and functional causes are merely proximate, Kitcher

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[7] Another avenue that Mayr might take is to suggest that narrative explanations involve answering "why" questions, but this seems rather controversial, at least with regard to species. Recall the No Lawlike Generalization argument from Chapter 3.

holds that structural inquiries may ask legitimate "why" questions. He says,

> "We should not confuse ourselves into thinking that one type of answer is appropriate to both types of questions or that one type of question is more 'ultimate' than the other. The latter mistake is akin to thinking of even numbers as more 'advanced' on the grounds that each odd number is followed by an even number." (1984a, p. 321)

Kitcher offers examples of "why" questions that one might ask when pursuing structural questions, such as "why does this virus have a protein coat of this type?" or "why does this virus only replicate on certain hosts?" The answers to these questions are traditionally used within an explanatory framework built around the delineation of natural kinds. In fact, the advocates of Process Structuralism, who represent part of the structuralist project, aim at developing a natural kind classification of forms.

Kitcher distinguishes three types of structuralist explanatory projects that provide good foundations for the development of structural based species classifications; those focusing on common genetic structures, common chromosomal structures, or common developmental programs. The approach taken by Kitts and Kitts (1979) as analyzed in Chapter 2 would represent an example of a structural project that focuses on common genetic structures. Also, Process Structuralism as analyzed in Chapter 2 is an example of a structural project that focuses on common developmental pathways.

Kitcher claims that although the temptation to reduce these three projects to a single genetic project may exist, such a reduction ought to be resisted. He draws an analogy from computer hardware and software to show the usefulness and difference between the various explanatory projects. It would seem worthwhile to divide computers into groups based on the internal hardware they possess. However, it would seem equally worthwhile to divide computer into groups based on the types of software they can run. Although more fundamental in some sense than a grouping of computers based on software capabilities, a grouping of computers based on internal hardware cannot ultimately replace a grouping of computers based on software capabilities. One cannot expect that a grouping of computer based on internal hardware will serve all our purposes. Similarly, Kitcher argues that biologists, such as the Process Structuralist, might divide organisms into species based on the possession of a common developmental program and we cannot expect that such a division will ultimately be reducible to a division based on supposedly more fundamental chromosomal or genetic structures. This is because developmental processes can arise from various genetic/chromosomal configurations. Hence, each structural division appears to serve separate, legitimate purposes.

Kitcher also identifies numerous historical explanatory projects that match up quite closely with some of the neo-Darwinian species concepts examined in Chapter 2. He claims there are two main principles used to generate historical taxonomies; the principle of continuity and the principle of division. The principle of continuity demands that the primary condition for determining taxa involve identifying a most recent common ancestor. The principle of division has three main versions each of which specifies conditions under which groups are to be viewed as distinct; reproductive, ecological, and morphological. He claims current species concepts are generated by determining the relative priority of the continuity and division principles. For example, advocates of the cladistic school focus on the continuity principle first and use the reproductive division principle secondarily to segment lineages. A phylogenetic species concept would appear to be the most acceptable to them. Alternatively, advocates of the evolutionary systematist school focus on the reproductive division principle first and use the principle of continuity secondarily to resolve borderline cases. A reproductive species concept or an evolutionary species concept would most likely be deemed acceptable by them.

The Inconsistency Objection Again: Disciplinary Discord

The fact that Kitcher's account of species pluralism mixes structural based species concepts with historical based ones raises an important series of questions. Has Kitcher included too many species concepts? Can his account adequately address the inconsistency objection? In particular, one wonders whether Kitcher's account includes concepts that are scientifically illegitimate, such as the structural based species concepts offered by Kitts and Kitts and the Process Structuralists. If a case can be made for why these are illegitimate, then Kitcher's account seems problematic. We will pay particular attention to whether a Process Structuralist species concept ought to be considered legitimate.

Recalling Beatty's discussion of the types of pluralism within biology, it would appear that Kitcher's account of pluralism embodies a bit of the all or nothing type when comparing structural and historical species concepts. The theoretical tension between these two types of species concepts can be identified more precisely by suggesting that Kitcher's account appears to suffer from what we will call disciplinary discord. Disciplinary discord occurs when two or more scientific disciplines or theories come into some type of conflict. The conflict can be said to occur in a number of ways, whether it involves a conflict between the theories, concepts, methods, or even objects of study embraced by advocates of the various disciplines or theories.

Knowing when disciplinary discord occurs requires being able to identify scientific disciplines. Bechtel (1986) offers a brief but helpful analysis of the units of science and how to identify them. He chooses to use the term 'discipline' to refer to the basic unit of science. He suggests there are three useful aspects of scientific disciplines that can be used to identify them. Scientific disciplines can be identified by their objects of study, their cognitive activities, and their social/institutional organization. We will hold that disciplinary discord occurs when scientific disciplines come into conflict in over one or more of the above three aspects.

In attempting to get a better grasp of what is meant by objects of study, Bechtel quotes Shapere (1984) who equates objects of study with domain. Shapere defines domain as "the set of things studied in an investigation." (p. 320) He also suggests that domains are not presented to scientists, rather scientists must decide which items to include in a domain. This is similar to our earlier comments from Chapters 1 and 2 about the species concept not being theory-neutral.

Bechtel notes that Shapere does not provide general criteria concerning object membership in a domain. This is because the criteria change as science changes. However, Bechtel suggests that identifying causal relationships is a popular way to bind objects together in a given domain. He also suggests looking at the relations that separate entities into different domains. One way of doing this is to distinguish a part-whole hierarchy which indicates levels of organization. An example would be the classificatory hierarchy starting with 'species' proceeding upward through 'phylum.' Similarly, one might start with 'species' proceeding downward through 'atom.'

Bechtel notes that more needs to be done to distinguish domains for three reasons. First, within any given level there is the possibility of multiple domains occurring. There are many domains at the organ level, each dealing with different organs. Second, entities are often involved in different phenomena and hence are involved in different domains. For example, muscle fiber might play a role in biochemistry, pathology, and physiology. Third, even if the domain is the same, different disciplines address the domain differently.

With regard to identifying cognitive activities of a discipline, Bechtel begins by quoting Whitely (1980) who describes this aspect of a discipline as

> "that abstracted set of norms and procedures which both govern and constitute what is done to what phenomena, in which cognitive setting, and how it is understood. It consists of the cognitive structures which, on the one hand, represent what is known and, on the other hand, constitute the resources with which to change and develop what is known." (p. 302)

In light of Whitely's analysis, Bechtel suggests the following cognitive factors contribute to the structure of a discipline; (1) laws and theories, (2) problems examined, and (3) methods of examining the problems.

Bechtel points out that laws and theories are helpful for identifying disciplines but that biology seems to lack numerous lawlike generalizations. He ultimately believes the central problems a discipline examines provide a stronger basis for identifying scientific disciplines. Bechtel notes that Darden and Maull (1977) develop the idea of a field in order to capture this aspect of a discipline. They define a field as

> "a central problem, a domain consisting of items taken to be facts related to that problem, general explanatory facts and goals providing expectations as to how the problem is to be solved, techniques and methods, and, sometimes, but not always, concepts, laws, and theories, which are related to the problems and which attempt to realize the explanatory goals." (p. 144)

Bechtel credits Kuhn (1970) for identifying tools, methods and techniques as important cognitive activities to be used when identifying a discipline. Scientists use certain conceptual tools unique to their discipline, they perform unique experiments and interpret the results in certain ways, and they may even argue in different, unique ways.

With regard to the social and institutional organization of scientific disciplines, Bechtel notes that sociologists of science ought to be credited for recognizing the impact of social and institutional factors. Basically, sociologists of science hold that scientific activity and progress are influenced by social and institutional factors. The Strong Programme holds an extreme view that all scientific activity and progress is the result of social and institutional factors, totally downplaying cognitive factors. A more moderate approach concedes that cognitive factors play a role, but that social and institutional factors must a play some role due to the acceptability of some version of the following two theses; the under-determination of theories and the theory-ladenness of observations. All sociologists of science hold that acceptance of these two theses precludes cognitive factors from being able to completely account for all scientific activity and progress.

We will concentrate more on the cognitive factors when discussing the discord between theories and disciplines underlying the two different types of species concepts in Kitcher's account. An important consideration when assessing whether discord occurs between disciplinary approaches involves determining whether the cognitive aspects of the approaches are incommensurable. Disciplines that have incommensurable cognitive aspects would likely exhibit a high degree of disciplinary discord. When disciplines utilize conceptual tools or methods that fail to match up cleanly with the conceptual tools or methods of the other disciplines, the cognitive aspects of each discipline are said to be incommensurable. It is as if the disciplines have completely different notions of what counts as a legitimate solution to a problem or field because of the radical differences in their cognitive aspects. Of course disciplinary conflict can occur in other ways, but we will contend that the type of conflict that a rather robust account of species pluralism like Kitcher's exhibits is related to the incommensurability between cognitive activities of more than one discipline.

Evidence of Discord in Kitcher's Species Pluralism

A clear example of incommensurability between cognitive activities of two disciplines occurs between a creationist view of species and an evolutionary view. Any account of species pluralism that embraces both of these approaches would exhibit disciplinary discord. "God" is a conceptual tool within a creationist view but not within an evolutionary view. Furthermore, there is no way to translate "God" into any meaningful conceptual tool within the evolutionary approach. What about Kitcher's account that incorporates both neo-Darwinian and structural species concepts? Whether or not his account exhibits disciplinary discord is less clear, but there seems to be some evidence to support the occurrence of such discord.

An initial indication that the two projects are in disciplinary discord can be found in the recent biological literature concerning the impact of Process Structuralism. Amundson (1994) suggests that the debate between structuralists and historicists such as neo-Darwinians is not semantic. He says, "The dispute is, at bottom, a clash of explanatory strategies, of approaches to explaining the nature of organic life." (1994. Reprinted in Hull and Ruse 1998, p. 96) Griffiths (1996) provides the following summary of the Process Structuralist project.

> "The process structuralist ideal is a periodic table of organisms or traits of organisms based on the generic forms......A new ideal for evolutionary explanation accompanies this new ideal of classification. Biological forms are to be explained by placing them in the periodic table of morphology rather than by tracing their history. Historical explanations are replaced by structural explanations." (1996, p. S4)

It would appear then, that the two projects each respectively aim to account for 100% of the domain in question on their own terms.[8]

Stronger evidence that the two disciplinary projects in Kitcher's account exhibit incommensurability between their respective cognitive aspects stems from the that fact that each project aims to develop completely different types of taxonomic hierarchies. The historical approach aims to develop systematic hierarchies of individuals or historical entities. The taxa in these respective hierarchies need to exhibit historical connectedness. The structural approach aims to develop a classificatory hierarchy of natural kinds. The

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[8] Although one may object that structural explanations are merely proximate whereas historical explanations are ultimate, *this is not what Kitcher claims.* He believes structural explanations are ultimate in their own sense. Wilkerson (1993) and Webster and Goodwin (1996) also suggest that historical explanations fail to explain structural explanations.

taxa in these hierarchies do not need to exhibit historical connectedness. Recall that the taxonomic hierarchies in Ereshefsky's account exhibit a slight conflict at the species level, yet the conflict dissolves as one proceeds up though the higher taxa. This is due to the fact that all taxa on his view ultimately fall in line with the process of descent. In Kitcher's account, it would appear that the conflict does not dissolve as one proceeds up through higher taxa, since the structural approach does not require that taxa follow the process of descent. Given that the structural approach allows for polyphyletic taxa, the taxonomic hierarchy of any structural approach and the taxonomic hierarchy of any historical approach will fail to match up cleanly with one another.

Another indication that there is incommensurability between the two disciplinary projects in Kitcher's account is the fact that each disciplinary approach appears to have a radically different conception of the term 'species.' Each of the historical projects sees species as individuals as indicated by the corresponding *systematic* hierarchy. Similarly, each of the structural based projects sees species as natural kinds as indicated by the corresponding *classificatory* hierarchy. Incommensurability appears to arise because the two different ontological views of species fail to translate into one another. Although neo-Darwinians like Sober believe viewing species as sets is merely a parlor trick in translation that can be done at anytime, it is hard to see how the polyphyletic species groupings identified by Structuralists can meaningfully be called individuals or historical entities. Furthermore, is would appear that each disciplinary approach sees different types of groups as species. The actual groups of organisms identified as species by both approaches often have vastly different makeups. This is indicated by the fact that neo-

Darwinians do not allow polyphyletic taxa whereas Process Structuralists would allow such taxa.

Wilkerson (1993) offers an analysis of a Kitcherian like species pluralism which supports the idea that there is discord between the two general approaches to species. Along the lines of Caplan (1980, 1981) and Kitts and Kitts (1979), Wilkerson argues that attempting to uncover the genetic causes of discrete and stable groups of organisms is a legitimate scientific endeavor. He believes such groups are rightly viewed as biological natural kinds. However, he distinguishes *between biological natural kinds* and *species*. He argues species are historical and suggests that biologists rightly conceptualize species in an individual/historical framework consisting of various populations giving rise to other populations. Hence, he argues in favor of two different types of biological inquiries. On the one hand, some biologists aim to explain the various biological kinds by citing the genetic causes of such kinds; on the other hand, some biologists aim to explain species by citing historical relations of descent from a common ancestor. In a sense then, Wilkerson advocates developing both a species taxonomy and a biological natural kind taxonomy.

It is interesting to note that Wilkerson believes that the account of natural biological kinds given by those studying genetic structures does different work than the account of species given by evolutionary biologists. Part of his reason for saying this is that the entities being explained by an account of natural biological kinds are much smaller groupings than traditional species. They must be, in order to have a somewhat uniform genetic structure. Recall that advocates of the species-as-individuals thesis argue that species must be individuals because they do not exhibit similar characteristics upon which to formulate general laws. Wilkerson suggests that biological kinds are much smaller classes of organisms than traditionally conceived. As a result, those interested in biological kinds are actually looking at wholly different entities than those who are interested in species. It would appear that there is a serious sense in which both disciplinary approaches are seeing different domains and utilizing different conceptual tools.

There may ultimately be a way of dissolving the apparent discord between the two approaches in Kitcher's account by integrating the two approaches in some way. However, *prima facia*, the discord poses a serious challenge to integration. We will examine the possibility of integration near the end of the chapter. For now, we will consider a more direct response to the apparent discord within Kitcher's pluralism.

Answering the Problem of Disciplinary Discord

When two or more scientific disciplines exhibit incommensurability between cognitive activities, and hence exhibit disciplinary discord, it would appear that three options are available for dealing with such discord; (1) science could proceed as best it could with each discipline carrying on along different pathways, (2) science could attempt to integrate the disciplines into one uniform theory, or (3) science could attempt to show that one theory is superior to the other(s). The integration of scientific disciplines involves the second option; the joining of two or more scientific disciplines into a single, uniform scientific discipline. The evolutionary synthesis between Darwinian theory and Mendelian genetics is often cited as an example of scientific integration. The question we are interested in is whether integration of various approaches to species is possible within a single account of species pluralism.

Prima facia there would appear to be some value in developing an integrated account of species pluralism that includes many theoretical and disciplinary interests. Such an account arguably promotes scientific understanding and progress. However, the possibility of progress within a pluralism as robust as Kitcher's might be seriously diminished if the account exhibits disciplinary discord. This is one reason why option (1) is frowned upon by almost all biologists. Some biologists suggest, along the lines of option (2), that it is possible to integrate so called developmental/structural interests into neo-Darwinism. We will examine below whether social and institutional factors might offer a possible avenue for easing the discord between the disciplinary approaches within Kitcher's rather robust account of species pluralism. But first, we will consider option (3) in more detail.

IV. The Anything Goes Objection

Hull (1987) and Ghiselin (1987) both complain that species pluralism is forced into an "anything goes" mentality such that legitimate, scientific taxonomic approaches cannot be discerned from illegitimate, unscientific ones. Hull remarks,

> "The greatest danger of pluralism is that it provides no means or even motivation for reducing conceptual luxuriance. Without such pruning, the integration of scientific knowledge is impossible. There has to be some reasonable middle ground between anything goes and the insistence that there is one and only one way to divide up the world and we know for all time what that way is." (1987. Reprinted in 1989, p. 121)

We will call this objection the anything goes objection. Hull suggests that it is better for biology to push the biological species concept for all it is worth rather than opening the doors to pluralism and having to be concerned with the inclusion of unscientific species concepts.

Ereshefsky (1995) offers a slightly different version of the anything goes objection. He understands that society has limited resources so not all species concepts can be explored. Pluralism, it is claimed, provides no way of choosing between species concepts. Hence, advocates of the anything goes objection argue that species concepts will be inadequately explored. Hence, Ereshefsky notes that advocates of species pluralism must provide criteria for choosing among species concepts (or for prioritizing among species concepts). The way Ereshefsky describes the objection makes the central issue more a matter of how to decide among concepts in the face of limited resources rather than a matter of which concepts are legitimate scientific species concepts. Although there is an important difference between Hull's way of phrasing the objection and Ereshefsky's way, the response Ereshefsky offers applies equally well to either his own or Hull's way of phrasing the objection.

The biggest concern for advocates of the anything goes objection involves the potential for including marginally scientific species concepts such as a creationist species concept. In addition, many contemporary biologists are concerned about including the structural based species concepts described by Kitcher. Ereshefsky believes he has a way to rule out the use of marginally scientific species concepts and ill-conceived species concepts such as the structural based ones. In the event that Ereshefsky can provide clear criteria for ruling out these non-Darwinian species concepts, it would appear that the potential problem of discord within species pluralism would be dissolved.

A normative naturalist response

Ereshefsky (1992, 1995) responds to the anything goes objection by giving some background on the nature of scientific taxonomy and then offering criteria that he believes any taxonomic approach must meet in order to be properly scientific. He rejects the attempt to provide a straight forward demarcation criterion á la Popper since he is skeptical that such a criterion can be clearly given. Instead of pursuing a demarcation criterion, Ereshefsky turns to normative naturalism to provide an answer to the anything goes objection.[9] Normative naturalism asserts there are three major components to scientific disciplines; general aims, methodological rules, and projects of inquiry. General aims are the main considerations of a discipline. For instance, all the sciences would likely hold that the pursuit of knowledge is the overriding general aim. Methodological rules are used to determine which project of inquiry within the discipline should be pursued. The methodological rules are chosen based on their ability to weigh whether or not a project will achieve the general aims of its discipline. Normative naturalism offers three ways of determining which methodological rules do this weighing the best; (1) use the history of science to judge past methodological rules, (2) use empirical evidence from the world, (3) perform a conceptual analysis to determine which rules would best achieve the aims of the discipline. Projects of inquiry revolve around specific explanatory or

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[9] Ereshefsky draws his views of normative naturalism from Laudan (1990), Rosenberg (1990), and Leplin (1990).

predictive aims, (e.g. attempting to explain the apparent discreteness and stability of groups of organisms).

Ereshefsky took a survey of the four main schools of taxonomy in order to determine the general aims and methodological rules of biological taxonomy.[10] He claims that they all agreed on one main aim;

> "To provide empirically accurate classifications that allow biologists to make inferences. Examples of such inferences are inferring the evolutionary history of a taxon, inferring the close relatives of taxon [sic], and inferring what traits the other members of a taxon typically have. The primary function of such inferences is to aid in the tasks of prediction or explanation." (1995, p. 384)

However, he claims they all disagreed on which methodological rules best achieve the general aim. For example, advocates of the biological species concept accept different methodological rules than advocates of the ecological species concept or the phylogenetic species concept. This fact results in numerous taxonomies of the organic world; a plurality of methodological rules gives rise to a plurality of taxonomies.

Ereshefsky points out that two types of principles are used to construct any taxonomy; sorting principles and motivating principles. "Sorting principles sort the constituents of a theory into basic units. Motivating principles justify the use of sorting principles." (1992, p. 682) Take for example the biological species concept. Its sorting principle says to sort species into groups that can interbreed and produce fertile offspring. The motivating principle that justifies this sorting principle is that interbreeding is the causal factor which produces lineages or groups that evolve as a unit.

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[10] He conducted the survey by examining introductory texts and journal articles.

Motivating principles refer to the causal processes that produce evolutionary units. As he says,

> "The interbreeding approach cites the process of interbreeding, the ecological approach highlights environmental selection pressures, and the phylogenetic approach focuses on the process of descent from common ancestry." (1992, p. 682)

Ereshefsky suggests that there could be universal laws about the types of basal taxonomic units such as biospecies, ecospecies, or phylospecies, but there are no universal laws about particular species.

In light of this brief analysis of taxonomy and normative naturalism, Ereshefsky suggests that four methodological rules best gauge whether a taxonomic approach can achieve the general aims of biological taxonomy:

(1) Motivating principles must be empirically testable.
(2) Sorting principles must produce only one internally consistent taxonomy.
(3) Motivating and sorting principles must be consistent with other well established scientific hypotheses.
(4) Motivating principles must be consistent with and derivable from the theory which the taxonomy is embedded in.

It is important to note that the third rule requires taxonomies to be consistent with evolutionary theory; the motivating and sorting principles should be extensions of what evolutionary theory suggests about the discreteness and stability of species.

Ereshefsky suggests the following measure for determining which taxonomic approaches are legitimate; those that meet all four rules should be pursued, those that meet none should not be pursued except as a last measure. The more rules an approach meets, the more justification biologists have for pursuing it. Ereshefsky embraces the fact that this boundary is vague. He again argues that vagueness is a part of biology and science. He also mentions that there are other rules that could be employed (i.e. simplicity, generality, stability, etc.), but he says these are merely pragmatic considerations. These are secondary rules that could be used in addition to the four primary methodological rules, but these secondary rules do not have to be used. For instance, he notes that the secondary rule stating that a taxonomic approach ought to be general might be at odds with the nature of the organic world; a single general approach may not adequately address the complexity of the organic world.

Not surprisingly, Ereshefsky argues that the various species concepts within his account of species pluralism reflect taxonomic approaches that meet all four methodological rules. Furthermore, Ereshefsky claims that these rules can be used to cast suspicion on a number of alternative taxonomic approaches. Consider the phenetic species concept. Ereshefsky claims such a species concept violates the second rule. As we saw in Chapter 2, a major criticism of the phenetic species concept was that it was possible for two different persons employing the phenetic species concept to develop two incompatible taxonomies of species with respect to any given group of organisms. The second criterion requires that the sorting principles provide an unambiguous methodology for determining species. Ereshefsky claims that a phenetic species concept fails to do this.

A creationist species concept would appear to violate the first, second, and third rules. There is no way to empirically test whether God is or is not the cause of species. Furthermore, the methodology of a creationist species concept is unclear so it would presumably violate the second rule. Lastly, a creationist species concept would appear to be inconsistent with evolutionary theory so the third rule is surely violated.

Ereshefsky also claims that typological species concepts (i.e. structural species concepts based on idealistic morphology, bauplan, developmental constraints, etc.) are suspect because they violate the fourth rule. Following Mayr (1963) and Sober (1980), he claims that typological thinking is inconsistent with evolutionary theory. Since typological/structural species concepts are not consistent with the tenets of neo-Darwinian evolutionary theory, he suggests they ought to be rejected. Ereshefsky claims that only species concepts which embrace the idea that species are historical entities are ultimately derivable from the tenets of evolutionary theory.

Problems for a normative naturalist response

There are some problems with Ereshefsky's response to the anything goes objection. First, it is not clear that all the species concepts Ereshefsky embraces avoid producing internally inconsistent taxonomies. Recall the problems with implementation of the history-based phylogenetic species concept that were discussed near the end of Chapter 2. The various species taxa derived from application of the history-based phylogenetic species concept are dependent upon numerous methodological decisions. It is not clear that a single, unique taxonomy can be derived purely from the idea that species are the smallest discernible groups of organisms exhibiting uniquely derived characters from a recent common ancestor. Far too many assumptions need to be made about what constitutes a character and how characters ought to be recognized/represented.

Ereshefsky might reply that the phylogenetic species concept, at the very least, does produce a single taxonomy *once the methodological decisions have been agreed upon* by those applying it, whereas structural based species concepts would still be plagued with inconsistency. This, however, seems overstated. Structural species concepts admittedly face the difficult question concerning how much similarity is enough. However, this need not be judged as a fundamental flaw. As Ereshefsky himself has argued at other times, precise boundaries in biology are not to be found. The fact that we are unable to lay out the boundaries of similarity with great precision fails to show that underlying structural causes are not at work. Furthermore, Ghiselin (1997) distinguishes between two different similarity measures; "overall similarity" and "over some similarity." He rightly rejects the former measure on the grounds that such a measure makes little sense.[11] However, he recognizes that "over some similarity" might actually provide a plausible basis for measuring similarity. He suggests that the grouping of hydrocarbons according to their molecular weight is an objective example of grouping entities based on some circumscribed set of properties. Problems with such measures of "over some similarity" only run into trouble when more than one kind of property is used to assess similarity and the property being measured is not circumscribed in some way. Rosenberg (1985) expresses a similar sentiment regarding structural species concepts. It is not so much that such species concepts are fundamentally flawed, rather it appears that all the approaches offered up until this point have been inadequate. In principle, he

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[11] See Sober (1993) for further support of this.

believes it is possible to develop structural species concepts that measure similarity in some way. Of course, Process Structuralists suggest their approach is testable and they challenge neo-Darwinians to develop equally testable measures of species. However, more experimentation will need to be done before Structuralists can claim to have solved the problem of measuring similarity.

Advocates of the biological species concept would appear to be faced with difficult judgments about similarity as well. This seems especially likely if the group of organisms under study by two different groups of biologists exhibit a serious amount of introgression. Although advocates of the biological species concept may all agree that species should be sorted according to their ability to interbreed, this methodological rule appears to be rather unhelpful in hybrid situations like those outlined by Stanford in Chapter 2. In light of the difficulties the second rule poses for species concepts that Ereshefsky embraces, it would appear that the second rule may need some revision, may need to be rejected, or may not always be required if all the other three rules are met.

One might argue that Ereshefsky's third rule is unduly conservative. Rather than allowing science to explore alternative explanatory frameworks Ereshefsky's third rule restricts science to a single approach; namely, a neo-Darwinian/genealogical one. Of course such a rule makes possible the rejection of a creationist species concepts (and other metaphysically suspect concepts). However, the third rule might actually constrain the progress of science.. This would not be good given that science has a long way to go toward attaining the truth about biological matters. Of course, Ereshefsky might reply that biology is close to the end of the line with respect to gaining such truth. However, Stanford (1995) argues that such a belief is unjustified. Stanford supports his argument by appealing to the numerous biological phenomena that lack sufficient explanation. All in all, the acceptability of the third rule hinges upon how far along we believe scientific inquiry actually is. Ereshefsky believes scientific inquiry is close to the truth about matters, whereas Kitcher and Stanford appear to believe it has a way to go yet. There does not appear to be a clear answer to this debate.

The biggest problem for Ereshefsky's normative naturalist response to the anything goes objection is his claim that structural based species concepts violate rule four. It would appear that he is wrong about this. Of course the structuralist based species concepts will fail the fourth rule if, as Ereshefsky suggests, the motivating principles of the structural based species concepts must be consistent with and derivable from neo-Darwinian theory. However, examining the fourth rule itself, it is unclear that structural approaches to species violate this rule. It is worth examining Ereshefsky's comments about the fourth rule directly. In reference to the fourth rule he remarks,

> "......the motivating principles of a taxonomic approach should be consistent with and derivable from the tenets of the theory for which the taxonomy is produced. In particular, a taxonomic approach in biological systematics should be derivable from well-established tenets in evolutionary theory. For example, in the case of the interbreeding approach, the motivating principle that interbreeding can cause stability in lineages should be an extension of what evolutionary theory tells us about the stability of lineages in general." (1992, p. 683)

He then uses this to reject structural based species concepts such as those offered by Ideal Morphologists and Kitcher. At one point, Ereshefsky claims that structural based species concepts such as those offered by advocates of Ideal Morphology (i.e. Process

Structuralists) ought to be rejected because the concepts are inconsistent with evolutionary theory. He says, "approaches based on idealistic morphology are illegitimate because they violate criterion 4." (1992, p. 684) Later on, he speaks directly of Kitcher's attempt to include structural based species concepts in an account of species pluralism. Ereshefsky argues that since evolutionary theory requires species to be historically connected, Kitcher's account of pluralism (more directly, the structural based species concepts he advocates) ought to be rejected. He says, "By allowing nonhistorical species concepts, Kitcher's pluralism falls outside the domain of evolutionary biology and should be rejected." (1992, p.688)

In essence, there is really nothing wrong with the fourth rule. It states a condition that is certainly important for a taxonomic approach to meet. However, there is a problem with Ereshefsky's use of the fourth rule to reject structural based species concepts. He interprets the fourth rule too narrowly. The phrase "evolutionary theory" is a rather ambiguous phrase. Ereshefsky interprets "evolutionary theory" in neo-Darwinian terms. In light of this, he is absolutely correct when he says the motivating principles governing structural species concepts fail to be consistent with and derivable from *neo-Darwinian* evolutionary theory. Also, he is absolutely correct when he says that nonhistorical species concepts fall outside the realm of *neo-Darwinian* evolutionary biology. However, by linking the term "evolutionary biology" with neo-Darwinism Ereshefsky begs the question. Evolutionary theory need not be interpreted in a neo-Darwinian way. As a matter of fact, advocates of structural based species concepts would reject common descent and natural selection as the primary mechanisms of evolution and offer an alternative mechanism. For example, Process Structuralists suggest that strongly entrenched developmental constraints (in the form of morphological and transformational "fields") are the cause of the apparent discrete and stable groups of organisms. Evolution occurs through transformations of the developmental constraints. Such a view is consistent with other current scientific theories. Process Structuralists recognize the importance of genetics and heredity, since these are the avenues which (1) help maintain the developmental constraints over time and (2) account for transformations in the constraints.

If we were to interpret the fourth rule from a Process Structuralist point of view, it would appear that the idea that developmental constraints are responsible for producing discrete and stable groups of organisms is consistent with and derivable from the Process Structuralist theory of evolution. Furthermore, as we saw in Chapter 3, only neo-Darwinian evolutionary theory requires that species be individuals, Process Structuralism has no such requirement. As a matter of fact, Process Structuralists prefer to think of species as natural kinds consisting of sets (or classes) with organisms as members. In light of this, it would appear that Ereshefsky's application of the fourth rule is a bit problematic.

Even though Ereshefsky's normative naturalist response to the anything goes objection rules out extremely suspect species concepts, it fails to show that all structural based species concepts, such as the one offered by the advocates of Process Structuralism, ought to be rejected. Hence, Kitcher's account of pluralism appears to survive Ereshefsky's normative naturalist response to the anything goes objection.

However, Kitcher's account needs to face other challenges that attempt to do away with structural based species concepts.

V. Other Challenges to Kitcher's Pluralism

Ereshefsky's normative naturalist response is merely one way to attempt to rule out structural based species concepts from an account of species pluralism. Griffiths (1996) offers another attempt that is actually independent of pluralistic concerns. In fact, Griffiths's argues directly against the Process Structuralist aim to develop a structural account of phylogenetic phenomena that is independent of neo-Darwinism. Hull (1987) offers another attempt that is aimed more directly against species pluralism of any sort. Although neither Griffiths or Hull support species pluralism, what they have to say with regard to structural or non-Darwinian projects is relevant to an assessment of a Kitcherian account of species pluralism.

Griffiths (1996)

Griffiths (1996) notes the difference between an historical approach and a developmental approach to accounting for the phenomenon of phylogenetic inertia. Phylogenetic inertia is the idea that lineages continue along their designated pathway until interrupted by some force. Basically, phylogenetic inertia manifests itself as discrete and stable groups of organisms; the very entities biologists eventually name as species. Neo-Darwinians account for this phenomenon through natural selection. Process Structuralists account for this phenomenon through developmental processes. His comments and analysis suggest that there is a degree of disciplinary discord between neo-Darwinians and

Process Structuralists. It would appear that both accounts utilize different conceptual tools and furthermore that only one of the two approaches can be correct.

Griffiths argues that the developmental processes and constraints identified by Process Structuralists are ultimately explainable via historical accident. He suggests that the current set of developmental mechanisms could have been one set among any number of different sets, but that evolutionary history via neo-Darwinian mechanisms determined the current set. He goes on to cite Wimsatt (1986) who has explored from a neo-Darwinian perspective how developmental processes have become entrenched over time. In effect, Wimsatt attempts to usurp the notion of developmental constraint from the Process Structuralists and make it a neo-Darwinian concept. Griffiths suggests that the only reason for accepting a Process Structuralist view of species is the claim that the current set of generic forms capture a large portion of "the space of biological possibility." He argues that paleontological data from the Cambrian period does not support this claim. He claims that analysis of the period shows there were a wide variety of different forms that failed to make it through the bottleneck which occurred. Griffiths concludes this shows that the current set of developmental forms were actually selected for. Hence, he claims that even though we may cite developmental processes to account for phylogenetic inertia, the reason the developmental processes originally came to be entrenched is ultimately neo-Darwinian (i.e. historical) in nature.

There is something a bit disconcerting about Griffiths's presentation of the debate over phylogenetic inertia between Process Structuralists and Darwinians. There is not anything necessarily wrong with what Griffiths says, but his approach to the problem is indicative of a mind set that many biologists have which is that everything can be historicized no matter the costs. His view is indicative of what Kitcher (1984b) calls genealogical imperialism. Basically, genealogical imperialism holds that every evolutionary phenomena ought to be understood from a genealogical or historical perspective. Such a view seems to unduly limit scientific understanding and progress since it seems to inadequately address evolutionary phenomena. For example, when Griffiths notes that Gould (1989) argues that chance is the primary reason why many forms did not make it through the bottleneck of the Cambrian Period, Griffiths responds by suggesting that at the very least the forms which occurred prior to the bottleneck were developmentally viable. He refuses to give up the idea that selection had something to do with the fact that many forms did not make it through the bottleneck. However, Griffiths's response is rather weak since the so called "viability" of the forms that did not make it through the bottleneck is arguably not well founded. One could arguably say that the forms that did not make it were not viable (because they did not live) and hence, not well entrenched forms.

It is important to keep in perspective Griffiths's choice of paleontological data in his attempt to discredit the Process Structuralist view. Such a catastrophic event as the bottlenecking that occurred at the close of Cambrian Period is a rather extreme example. It is not clear which of the following played the primary role in producing the set of forms after the bottlenecking event; selection, development, or even chance. Griffiths's position would be better supported were he able to cite a more straightforward example of how some forms failed to pass through a clearly identifiable selective bottleneck. We will not be able to address whether such straightforward examples exist. Such an endeavor would appear to be a rather involved empirical research project. All in all, Griffiths's attempt to use paleontological data to support the sole use of the neo-Darwinian approach when accounting for phylogenetic inertia is inclusive.

Hull (1987)

Hull (1987) presents a formidable argument against species pluralism and against non-Darwinian approaches to species. Basically, he suggests that science is better off when it is monistic. Given Hull's penchant for the biological species concept it may come as no surprise that he believes that biologists should put all their marbles in one bag; namely, the genealogical one. Furthermore, he claims that if we accept pluralism too early, we might fail to stumble upon the correct monistic theory that would actually unify all our inquiries. Hull says, "the only way to find out how adequate a particular concept happens to be is to give it a run for its money." (1987. Reprinted in 1989, p.121) In a sense, Hull suggests that we ought to give monism a bit more time. He believes that choosing a concept and "pushing it for all its worth" is the best scientific approach.

Beatty (1997) offers a number of interesting responses to this objection. First, Beatty claims that a monistic approach can actually give scientists an inflated view of their theory. This may result in an inability to see the limitations that face their theory. He cites Crow (1979) who claims that non-Mendelian segregation of alleles might be more common than supposed, but it is not noticed because scientists simply do not look for such a phenomena. This is reminiscent of Kitcher's suggestion in Chapter 3 that biologists have failed to find lawlike generalizations because they have looked in the wrong places in light of accepting just a genealogical framework.

Relatedly, Beatty claims that pluralism may actually help generate progress in science. If the only thing science aimed to do was tally repeated instances in favor of a theory, science would not be as attractive to newcomers who are able to develop new, fruitful theories. He believes pluralism has a positive effect on the ability of science to move forward. He also notes that prizes and awards in science are often given to alternative theories that appear to conflict with more established theories. This fact would appear to suggest that science values maverick ideas that push the envelope.

These two responses offered by Beatty appear to accept that an answer to the debate between monists and pluralists involves sorting out which mistake is worse; accepting pluralism too early or blinding ourselves to alternative theories that may provide insight. Neither response values pluralism because it best captures the underlying complexity of species. A more direct response to Hull's objection is that certain domains in biology are messy and complex, and in turn, require a pluralistic approach. If the underlying processes are not monistic in nature, then it would appear that a monistic approach is inappropriate. This appears to be the main reason why Ereshefsky and Kitcher both offer their respective accounts of species pluralism. Species pluralism is not a passing fad for Kitcher or Ereshefsky, it is here to stay. No matter how much knowledge we gather about the organic world, species pluralism will be necessary because the underlying biology of species is messy and complex.

In order to assess the merit of Hull's position, it is necessary to be clear about which variant of species pluralism is being set in opposition to Hull's call for species monism. Recall that Beatty distinguishes between the all or nothing type of pluralism and relative significance disputes. In addition to these, we noted that Ereshefsky's species pluralism might represent a third general variant; one which accepts an all or nothing debate at a lower taxonomic level, but not at the higher taxonomic levels. It appears that Hull might be receptive to an account of species pluralism like Ereshefsky's. Although Hull is an advocate of the biological species concept, he is also an advocate of the more general genealogical approach to understanding evolutionary phenomena. What Ereshefsky seems to suggest is that correctly understanding evolutionary phenomena requires acceptance of species pluralism at the basic taxonomic level, but it requires genealogical monism at a more general level. Ereshefsky and Beatty both suggest that scientific progress and understanding are bolstered by the acceptance of pluralism. But they do not have in mind the type of pluralism that involves all or nothing disputes, and this is the type of pluralism that Hull appears to be arguing against when he suggests biology ought to push the genealogical view for all it is worth. So, it would appear that Ereshefsky (and Beatty) might accept Hull's argument for a type of *genealogical* monism which could be used against a Kitcherian account of species pluralism.

The Possibility of Integrating Structuralism and neo-Darwinism

Although the call for monism of a genealogical type accepts that species pluralism is necessary to some degree, the issue of whether or not structural species concepts ought to be included in an account of species pluralism still needs to be addressed. Advocates of structural species concepts could arguably hold that even genealogical monism fails to capture the complexity and actual messiness of the underlying biology of species. Of course, if structural species concepts are at odds with historical species concepts in the sense of an all or nothing dispute, then given the usefulness of neo-Darwinism and its associated historical species concepts, there would appear to be some reason to continue solely pushing a neo-Darwinian approach to species (or pushing two separate, discordant approaches to species).

However, advocates of a Kitcherian account of species pluralism have one last possibility for giving their account some legitimacy. We need to assess whether there is some way structural concerns could be integrated with neo-Darwinian concerns without the account collapsing into an all or nothing dispute. Such an approach would apparently require that both the advocates of Structuralism and the advocates of neo-Darwinism soften their positions to allow for some degree of interdisciplinary exchange.

Recall that the problem with Kitcher's account is that it appears to embody disciplinary discord. Such apparent discord results in an inability to work toward progress. Making progress requires that everyone involved engages in the same cognitive activities so that there is a clear measure of when progress is being made. Two disciplines that are in discord fail to measure progress in the same way because they have different standards for measuring progress. The question we are considering now is whether structural species concepts can be included in an account of species pluralism without discord occurring.

Gould and Lewontin (1978) discuss a related issue. They consider how developmental constraints upon organisms at the microevolutionary level can be addressed given the near stranglehold the adaptational programme has on evolutionary biologists. Gould and Lewontin suggest that evolutionary biology unjustifiably uses adaptational stories at the expense of developmental constraints when attempting to account for traits in organisms. They do not argue for the overthrow of the adaptational programme, rather they suggest that it make room for developmental constraints. The Process Structuralists' claims about developmental constraints might be phrased in a similar way. Instead of suggesting that transformational fields replace neo-Darwinian species concepts, Structuralists might suggest that developmental constraints in general receive more attention.[12]

The trick to any type of integration is to utilize enough aspects from all the parts being integrated so that one can truly say integration has occurred. Since the cognitive tools of both the neo-Darwinian and Process Structural approach appear to be different, there might be some difficulty in integrating both approaches. A legitimate concern for structuralists is that any attempt to integrate with neo-Darwinians would require structuralists to give up some of its conceptual tools, since a neo-Darwinian approach to macroevolutionary phenomena is still considered primary. For example, in terms of cognitive tools, in order to get both approaches to mesh effectively, the Process

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[12] See Part III of *Integrating Scientific Disciplines* (1986) for articles relating to how developmental and structural concerns can be integrated into the neo-Darwinian Evolutionary Synthesis. See also Smith (1992).

Structuralists might have to drop some of their jargon such as "transformational fields" and "generative processes" in favor of more neo-Darwinian friendly terminology like developmental constraints. However this concern of structuralists might be soothed if neo-Darwinians conceded the idea that species can be completely accounted for through historical narratives.

In order to understand how neo-Darwinians might do this without completely giving up their own conceptual tools, we need to review how neo-Darwinians and Process Structuralists each account for stable and discrete groups of organisms. Recall in Kitcher's account of species pluralism that both the historical and structural approaches aim to give their own types of accounts of species. The historical approach focuses on giving narratives whereas the structural approach focuses on uncovering lawlike generalizations. As a result, each approach appears to be talking about completely different types of entities, even though they each use the term 'species.' Wilkerson (1993) picks up on this difference and suggests that those interested in structures (he is concerned with genetic structures but nothing precludes his position from applying to developmental structures) actually aim to pick out biological natural kinds, whereas those interested in relations between populations aim to pick out species. The upshot is that an historical approach uses narratives to explain species, whereas a structural approach uses generalizations to explain species (i.e. biological kinds).

Ghiselin (1997) makes some comments regarding the simultaneous use of narrative explanations and more lawlike explanations which might provide some insight into how neo-Darwinians might embrace a structuralist approach to explanation. He suggests that both types of explanation are important to the biologist. Historical narratives provide the biologist with details that are important for making generalizations. If evolutionary biology can find a way to utilize the narratives about lower level taxa like biospecies, evospecies, and phylospecies, etc. as evidence for more generalized claims about constraints upon slightly higher taxonomic levels, then it would appear that the integration of the two disciplinary approaches is possible. For example, although Process Structuralists talk about all taxa as if they are controlled by transformational fields and developmental processes, it might be better to suggest that such constraints merely provide a general framework within which particular species develop. The final outcome of particular species would be determined according to the types of neo-Darwinian mechanisms they are exposed to. Accordingly, the Process Structuralist approach would not be about species directly, but it would definitely have an impact on the final outcome of species. Although neo-Darwinian mechanisms would be used to characterize each species in particular, all species would be governed by the principles of the Process Structuralists.[13]

Such an integrated view might lend more objectivity to higher taxa which are currently viewed by neo-Darwinians as merely determined by conventional and pragmatic considerations. The objectivity would be provided by the identification of developmental constraints that act upon various organisms within a given higher taxon. As one were to move up the taxonomic hierarchy from genera to phylum, the number of constraints

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[13] Smith (1992) appears to suggest something similar to this.

governing a given taxonomic level would presumably become less and less. Of course this brief description of how both approaches might be integrated is sketchy. However, the fact that neo-Darwinians attempt to account for species through the use of historical narratives whereas Process Structuralists attempt to account for species and all other taxa through the identification of shared properties and the development of generalizations might be taken as evidence in favor of such integration.

We might also briefly examine how the creation of interdisciplinary social and institutional organizations might impact and direct the nature of integration between a neo-Darwinian approach and a structural approach. As it stands, each approach appears reluctant to work with the other. Webster and Goodwin (1996), two of the most prominent Process Structuralists, call for a complete rejection of the neo-Darwinian paradigm. Staunch defenders of neo-Darwinism, such as Griffiths (1996), seem unwilling to countenance any type of developmental or structural impact on species. With battle lines drawn so firmly, it is no wonder integration seems near impossible.

It would appear that the development of a joint project to assess the impact of structural and genealogical factors upon a tightly controlled population of organisms would help the cause of integration. Following up on a suggestion by Smith (1992), biologists from both approaches might first work together to identify a group of organisms for study that have a known and manageable genome which each side is comfortable working with. Then different types of experiments could be run on the group to assess whether the organisms are subject to structural constraints or selective pressures. For example, the group of organisms might be split into smaller groups and each group then subjected to a unique environment and allowed to breed over a series of generations. Structural constraints might be reflected in constant gene patterns in the genome of each organism in the last generation of each environment. The fact that such gene patterns fail to break up might be evidence that there is a Kitcherian like structural constraint that simply cannot be removed without resulting in the destruction of the organism. Of course, such evidence is merely inductive since the future could prove the experiment wrong, but this problem is faced by every type of scientific experiment. It is not a problem unique to structural-oriented experiments. Another type of experiment both approaches might investigate involves subjecting a polyphyletic group of organisms which structuralists believe is governed by structural constraints to experimentation. The polyphyletic group could be split into smaller groups and then each small group exposed to unique environments to assess whether different traits develop in each group over a series of generations. If different traits develop within each small group, this might be an indication that the original polyphyletic group was not governed by a structural constraint. If the groups stay fairly constant, this might indicate an underlying structural constraint is governing the original polyphyletic group. Although this suggestion for a joint experiment is sketchy, it seems to contain the seeds of what type of joint experimentation needs to occur in order to help along the cause of integration.

All in all it appears that in order for integration to be possible, neo-Darwinians need to be more open to developmental and structural research projects. Such openness needs to be reflected not only in the relaxation of the control over cognitive tools but also in terms of the willingness of neo-Darwinians to work with structuralists on joint projects. Neo-Darwinians arguably dictate the direction of evolutionary research; the descriptive study of taxonomists by Ereshefsky (1995) seems to be an indication of this. Until such openness is granted, a complete and fair assessment of integration is unlikely.[14]

VI. Summary

It would appear that of the three options available to evolutionary biologists when considering what to do in light of the apparent disciplinary discord that comes with a Kitcherian version of species pluralism, the integration option is the most attractive. Of course, a Kitcherian version needs to address the issue of whether and how integration between neo-Darwinism and Process Structuralism is to occur, but such integration does not seem inconceivable. Hull, Griffiths, and Ereshefsky hold that integration is not worthwhile, but their position may not best promote scientific understanding and progress; they may ultimately blind themselves to important evolutionary forces by refusing to consider structural concerns. Certainly they are right to insist that the structural concerns ought not give rise to disciplinary discord when juxtaposed with neo-Darwinian interests. They might even be correct in saying that neo-Darwinian interests take precedent over structural concerns when it comes to identifying species. However, as discussed above, the possibilities for integration seem plausible if not scientifically important.

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[14] It would appear that sending more funding in the direction of joint experiments and developing interdisciplinary conferences are important means of determining whether full integration is possible.

All in all, species pluralism is a necessary approach to a complete understanding of species. Furthermore, it would appear that a Kitcherian account of species pluralism which includes structural concerns as well as historical/genealogical concerns when it comes to understanding species ought to be accepted. Although a Kitcherian account has the appearance of giving rise to disciplinary discord, there appears to be some promise in integrating the apparently discordant concerns. Certainly, a concentrated effort by advocates of both neo-Darwinism and Process Structuralism to integrate their respective concerns will help establish an integrated approach to species. Even if complete integration is not possible, it would appear to be a greater mistake to reject the attempt to integrate than to attempt integration.

SUMMARY AND CONCLUSIONS

The primary aim of this dissertation has been to suggest an appropriate account of species pluralism for use within evolutionary biology; an account that incorporates a wide variety of theoretical interests while avoiding disciplinary discord. It is important to understand that the two accounts of species pluralism examined in this dissertation do not hold that species pluralism is just a passing fad that will become unnecessary once we get to the truth about matters. Both accounts hold that species pluralism is necessary in order to properly account for the nature of entities labeled as species; the underlying biology of these entities is so complex that a single species concept is unable to adequately account for every single grouping phenomena that evolutionary biologists identify as a species. Whatever else happens, species pluralism is here to stay.

Determining which account of species pluralism to accept is difficult because of the vast amount of theoretical interests that could potentially be included in an account of species pluralism. Advocates of species pluralism will want to aim for a pluralism that includes a sufficient number of species concepts to account completely for the entities labeled as species, yet does not suffer from disciplinary discord. The problem is captured more precisely in the following conditionals. If species pluralism is limited to a small set of species concepts in order to improve disciplinary uniformity, it may fail to adequately address the wide array of biological situations and casual processes. If species pluralism includes a wide variety of species concepts, there is a worry that the various species concepts might not fit neatly within a single disciplinary framework. After a thorough examination of two representative accounts of species pluralism, it appears that a

Kitcherian account of species pluralism is most desirable. Although a Kitcherian account of species pluralism exhibits some degree of disciplinary discord, it is better to aim to integrate the parts in discord rather than reject a Kitcherian account outright. A brief review of how we arrived at this conclusion is as follows.

I. Review of the Chapters

In Chapter 1 we noted that the attempt to develop a species concept aims to account for the discreteness and stability of groups of organisms. In light of this, we discussed two important roles species are thought to play in contemporary evolutionary biology. We noted that species play the role of basal taxonomic units as well as the role of units of evolution. We suggested that proper understanding of these roles was important for understanding many of the points throughout the rest of the dissertation.

In Chapter 2 we reviewed the problem of defining species. We found that this definitional problem has been rather intractable because each species concept examined fails to adequately address some important biological consideration. We examined a phenetic approach to species, four neo-Darwinian species concepts (the biological species concept, the ecological species concept, the evolutionary species concept, and the phylogenetic species concept) as well as two non-Darwinian species concepts (a genetic approach and a structural approach). We concluded the chapter by arguing that acceptance of some account of species pluralism is necessary in order to adequately capture and understand the complex nature of species. We also noted the that beginnings of the problem of discord arise with the consideration of non-Darwinian species concepts because non-Darwinian concepts stem from a different theoretical framework than neo-Darwinian species concepts.

In Chapter 3 we began to lay a foundation for why there is a potential for discord between historically-oriented species concepts and structural-based ones. We reviewed the philosophical problem surrounding the ontology of species. We identified and critically examined two specific arguments in favor of the species-as-individuals thesis; the *No Lawlike Generalizations* argument and the *Evolutionary Term* argument. We concluded that from a neo-Darwinian perspective it makes the most sense to say species are individuals because neo-Darwinian mechanisms require that the groups of organisms identified as species are historically connected. However, we also found that from a non-Darwinian perspective, such as a Process Structuralist approach, it is preferable to view species as sets or classes of organisms. This is because non-Darwinian species concepts refer to mechanisms that do not require that species be historically connected. We concluded the chapter by arguing that the ontology of species is largely dependent upon one's theoretical leanings.

In Chapter 4 we distinguished between various types of species pluralism and critically examined two accounts which hold that species pluralism results in the use of multiple taxonomies; one offered by Ereshefsky (1992) and one offered by Kitcher (1984a, 1984b, 1989). We also discussed the nature of pluralism in biology in general as well as the nature of disciplinary discord in science. These discussions helped show how both accounts of species pluralism appear to suffer from disciplinary discord. However, we argued that the potential for discord is much greater for Kitcher's account than for

Ereshefsky's account, since Kitcher's account includes structural based species concepts whereas Ereshefsky's does not. We discussed various attempts to alleviate the potential tension in a Kitcherian account which aim at rejecting the use of structural species concepts, but found that outright rejection of structural concepts is unwarranted and might be detrimental to scientific understanding and growth. We suggested that it might be better to aim to integrate structural and historical approaches, instead of rejecting one or the other. We noted that the discord facing a Kitcherian account of species pluralism is similar to the discord described by Gould and Lewontin (1978) between adaptationalists and developmentalists and might be dealt with in a similar manner. We argued that the discord within a Kitcherian account of species pluralism might be alleviated by broadening the scope of the conceptual tools used by both neo-Darwinians and Process Structuralist, attempting to develop some interdisciplinary research projects, and creating some interdisciplinary conferences and organizations.

II. Important Points of the Dissertation

There are three main points we have attempted to make in this dissertation; two have been underscored repeatedly throughout the dissertation, and a final one arises near the end when reflecting upon the possibility of integrating historical and structural approaches to species. First, species pluralism is a requirement for evolutionary biology. Second, the account of species pluralism we adopt ought to be Kitcherian in spirit, but it ought to aim at integrating neo-Darwinian species concepts and Structuralist species concepts. Lastly, the advocates of neo-Darwinism need to allow more consideration of non-Darwinian mechanisms and concerns when accounting for the nature of species. All of these points deserve some brief commentary.

With regard to the first point, species pluralism is a requirement because the nature of the entities biologists label as species is so complex that proper understanding of the maintenance (as well as evolution) of these entities requires reference to multiple causal processes. Species pluralism will not go away after we obtain the so called truth about the nature of these entities we call species. Biology is stuck with species pluralism, like it or not. Adopting species pluralism contributes to scientific progress since it provides a deeper, albeit more complex, understanding of the nature of species. Although there may still be some details to work out, such as how to deal with conceptual and institutional/organizational differences, the adoption of species pluralism is a step in direction toward deeper scientific understanding, and ultimately, scientific progress. Of course, this requirement to adopt species pluralism requires us to choose an acceptable account of species pluralism. This brings us to the second main point of this dissertation.

It would appear that a Kitcherian account of species pluralism is the best alternative for evolutionary biology, but it is only so with the understanding that evolutionary biologists aim to integrate historical based species concepts with structural based species concepts. It would appear that both type of concepts offer important insight into the nature of species and higher taxa. However, Kitcher's portrayal of such an account of species pluralism leaves many questions unresolved, the most important of which involves how to integrate both historical and structural species concepts underneath one uniform approach so that disciplinary discord is not a problem.

A few suggestions were made at the end of Chapter 4 about how evolutionary biologists might work toward integrating historical and structural species concepts. Reviewing these suggestions will help bring out a final point this dissertation aims to make. First, it was suggested that neo-Darwinians and Structuralists relax some of their jargon in an attempt to integrate both types of explanatory approaches to those entities recognized as species. We suggested that this might involve modifying the current set of conceptual tools utilized by evolutionary biologists so that the tools mesh together in the following way. The narratives developed by neo-Darwinians might be useful in developing lawlike generalizations about constraints which govern various types of species. For example, it was suggested that the developmental constraints identified by Process Structuralists might provide a general framework within which species are said to develop. The final outcome of particular species would be determined according to the types of neo-Darwinian mechanisms they are exposed to. Although the Process Structuralist approach would not be about species directly, it would definitely have an impact on the final outcome of those groups of organisms identified as species. So, neo-Darwinian mechanisms would be used to characterize each species in particular and all taxa (species included) would be governed by the principles of the Process Structuralists. We also suggested that such an integrated view might lend more objectivity to higher taxa which are currently viewed by neo-Darwinians as merely determined by convention and pragmatic considerations. The objectivity would be provided by the identification of developmental constraints that act upon various organisms within a given higher taxon. Furthermore, we suggested that both approaches aim to develop mutually acceptable research projects so as to test and develop an integrated approach to species. We offered sketches of two possible research projects; one involving a neo-Darwinian species grouping which is tested to see if it exhibits Structuralist ideas and another involving a Structuralist species grouping which is tested to see if it exhibits neo-Darwinian ideas. Finally we suggested that both sides work to develop interdisciplinary institutions and organizations that promote the sharing of information and dissemination of knowledge.

The difficulty facing integration may not really be as cognitive as it appears. The problem of integration may ultimately stem from the reluctance of neo-Darwinians to embrace an integrated approach. Hull (1989), Ereshefsky (1992, 1995), and Griffiths (1996) all espouse a rather hegemonic, neo-Darwinian approach to species which makes integration quite difficult. Not only do they all suggest that neo-Darwinian mechanisms are able to completely account for the nature of the grouping phenomena recognized as species, they also suggest that whenever a neo-Darwinian account fails, another one ought to be offered in its place. Mayr (1942, 1961, 1963, 1969) has long been the patron saint of the historical approach, suggesting that the historical approach is the only legitimate approach to understanding evolutionary phenomena. This neo-Darwinian reluctance might help explain the strong stance taken by Process Structuralists.

This suggestion about the reluctance of neo-Darwinians to accept non-historical explanations of evolutionary phenomena brings us to the point. Neo-Darwinians must forego such a hegemonic approach to understanding the nature of species if integration is to occur smoothly. Gould and Lewontin (1978) suggest this neo-Darwinian approach to traits in organisms is detrimental to a full understanding of the evolution of organisms within a species. Similarly, but at a macroevolutionary level, it would appear that a rather hegemonic neo-Darwinian approach to the maintenance and evolution of species contributes to an incomplete understanding of the grouping phenomena ultimately recognized as species. Evolutionary biologists ought to consider more fully non-Darwinian (i.e. structural) mechanisms and this requires that the historical view of evolutionary phenomena be relaxed a bit. It would appear this is a necessary condition in order for a Kitcherian account of species pluralism to ultimately be considered acceptable by both neo-Darwinians and Structuralists.

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