



Species

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SPECIES*

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I defend a view of the species category, *pluralistic realism*, which is designed to do justice to the insights of many different groups of systematists. After arguing that species are sets and not individuals, I proceed to outline briefly some defects of the biological species concept. I draw the general moral that similar shortcomings arise for other popular views of the nature of species. These shortcomings arise because the legitimate interests of biology are diverse, and these diverse interests are reflected in different legitimate approaches to the classification of organisms. In the final section, I show briefly how the pluralistic approach can help to illuminate some areas of biological and philosophical dispute.

1. Pluralistic Realism. The most accurate definition of 'species' is the cynic's. Species are those groups of organisms which are recognized as species by competent taxonomists. Competent taxonomists, of course, are those who can recognize the true species. Cynicism is attractive for the weary systematist who despairs of doing better. But I think that philosophers and biologists need not despair. Despite the apparently endless squabbles about how species are to be characterized, it is possible to defend an account of the species category which will do justice to the insights of several divergent approaches.¹

I shall try to explain a position about species that I shall call *pluralistic realism*, and to indicate in a general way why I think that this position is true. In particular, I want to defend four theses.

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¹Several—but not all those that have figured in the recent taxonomic literature. In particular, I hold no brief for phenetics.

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- (1) Species can be considered to be sets of organisms, so that the relation between organism and species can be construed as the familiar relation of set-membership.
- (2) Species are sets of organisms related to one another by complicated, biologically interesting relations. There are many such relations which could be used to delimit species taxa. However, there is no unique relation which is privileged in that the species taxa it generates will answer to the needs of all biologists and will be applicable to all groups of organisms. In short, the species category is heterogeneous.
- (3) The species category is heterogeneous because there are two main approaches to the demarcation of species taxa and within each of these approaches there are several legitimate variations. One approach is to group organisms by structural similarities. The taxa thus generated are useful in certain kinds of biological investigations and explanations. However, there are different levels at which structural similarities can be sought. The other approach is to group organisms by their phylogenetic relationships. Taxa resulting from this approach are appropriately used in answering different kinds of biological questions. But there are alternative ways to divide phylogeny into evolutionary units. A pluralistic view of species taxa can be defended because the structural relations among organisms and the phylogenetic relations among organisms provide common ground on which the advocates of different taxonomic units can meet.
- (4) Pluralism about species taxa is not only compatible with realism about species. It also offers a way to disentangle various claims that can be made in maintaining that “. . . species are real entities existing in nature, whose origin, persistence, and extinction require explanation” (Eldredge and Cracraft 1980, p. 15).

I do not intend to provide a complete defense of all these claims. I shall concentrate primarily on the first three theses, saying little about the issue of realism about species, although I hope that my explanations of theses (1)–(3), together with the discussion in Section 5, will make it possible to see how to avoid the charge that species are merely fictions of the systematist’s imagination.²

²The person who comes closest to advocating a realistic version of pluralism about species is John Dupré (1981), who defends what he calls (borrowing a name from John Perry) “promiscuous realism”. Dupré’s defense is brief (since the primary concern of his (1981) is to address some important issues in philosophy of language) and, to my mind, unconvincing. Pointing out that biological taxa cut across the divisions of organisms introduced by gastronomes hardly shows that there are alternative sets of kinds internal to biology. Nor does it help to note (1981, p. 83) that ecologists use the concept of population, for

2. Sets versus Individuals. My first thesis seems banal. After all, who would think of denying that species are sets of organisms? However, a number of philosophers and biologists—most prominently, David Hull and Michael Ghiselin—have recently campaigned against the notion that species are (what they call) “spatio-temporally unrestricted classes” and they have urged that species should be viewed as individuals.³ Strange though this proposal may initially appear, it cannot be lightly dismissed. Hull and Ghiselin argue that their account of species is far more consonant with our current understanding of the evolutionary process than the view that they seek to replace.⁴

Let me begin by explaining what I take to be the commitments of the traditional idea that species are sets. First, there is no inconsistency in claiming that species are sets and denying that the members of these sets share a common property. Unless ‘property’ is used in an attenuated sense, so that all sets are sets whose members share one trivial property—namely, the property of belonging to that set—then there are sets whose members are not distinguished by any common property. In particular, believing that species are sets does not entail believing that there is some homogeneous collection of morphological properties such that each species taxon is the set of organisms possessing one of the morphological properties in the collection. So we can accept (1) while endorsing Mayr’s celebrated critique of the morphological concept of species (Mayr 1942, 1963, 1969, 1970, 1982).

Let me now turn to the main arguments that have been offered for thinking that the view of species as sets is at odds with our best biological theorizing. One of these arguments claims that construing species as sets is incompatible with the doctrine that species evolve.⁵ Here is the starkest

this does not indicate any commitment to alternative species taxa. Hence, although I find Dupré’s short discussion of promiscuous realism provocative, I don’t think he has made out a case for this view.

³*Loci classici* are Ghiselin (1974), Hull (1976, 1978, 1980); Rosenberg (1981) provides a helpful summary. My discussion will be directed primarily at the arguments advanced by Hull. To the best of my knowledge, Ghiselin deserves credit for his original presentation of the thesis that species are individuals, but Hull’s articles are more systematic and detailed in arguing for the thesis.

⁴An exhaustive evaluation of this claim would require discussion of the merits and shortcomings of main features of phylogenetic systematics (cladism). This is undertaken in *Species*. For reasons of space, I have concentrated here on the main philosophical arguments.

⁵Another general worry about construing species as sets was voiced by Elliott Sober. As Sober rightly points out, his own existence is not essential to the existence of *Homo sapiens*: there are worlds in which Sober does not exist but in which the species does exist. Hence, he contends, the species is not to be identified with the set of humans. I reply that this conclusion does not follow. In different worlds, *Homo sapiens* is a different set. Just as the extension of ‘car’ varies from world to world, so does the referent of ‘*Homo sapiens*’.

version:⁶ “Species evolve. Sets are atemporal entities. Hence sets cannot evolve. Therefore species are not sets.” Quite evidently, there is a fallacy here, the fallacy of incomplete translation. It would be futile to think that mathematicians need to revise their standard ontology because of the following argument: “Curves have tangents. Sets of triples of numbers are nonspatial entities. Hence sets of triples of real numbers cannot have tangents. Therefore curves are not sets of triples of real numbers.” The correct response to the latter argument is to insist that, in the reduction of geometry to real arithmetic, the property of being a tangent is itself identified in arithmetical terms. Once the property has been so identified, it is possible to see how sets of triples of real numbers can have it. Only incomplete translation deludes us into thinking that sets of triples of real numbers cannot have tangents. An exactly parallel response is available in the case of species.

Assume, for the sake of the present argument, that a species is a set of organisms consisting of a founder population and some (but not necessarily all) of the descendants of that population. I make this assumption in order to show that there is a set-theoretic equivalent of the approach to species that Hull favors. 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.⁷ To say that the species gives rise to a number of descendant species is to claim that the founding populations of those descendant species consist of organisms descending from the founding population of the original species. By proceeding in this way it is relatively easy to reconstruct the standard claims about the evolutionary behavior of species.

A second major theme in Hull’s attack on the tradition is his suggestion that recognizing species as individuals will enable us to understand why there are no biological laws about particular species.

If species are actually spatio-temporally unrestricted classes, then they are the sorts of things which can function in laws. “All swans are white,” if true, might be a law of nature and generations of philosophers have treated it as such. If statements of the form “Species X

⁶In fairness to Hull, I should note that he does not advocate any argument that is as stark as the one presented here. However, he sometimes comes very close: see, for example, his 1981, p. 146.

⁷As Bill Fink pointed out to me, this allows for relatively trivial changes—such as chance fluctuations in frequency—to count as cases of evolution. Quite evidently, one can attempt to circumscribe the “genuine forces” of evolution, and use the resultant characterization to generate a more stringent conception of evolutionary change. Any such conception can easily be applied to the present context.

has property Y" were actually laws of nature, one might rightly expect biologists to be disturbed when they are proven false. To the contrary, biologists expect exceptions to exist. At any one time, a particular percentage of a species of crows will be non-black. No one expects this percentage to be universal or to remain fixed. Species may be classes, but they are not very important classes because their names function in no scientific laws. Given the traditional analyses of scientific laws, statements which refer to particular species do not count as scientific laws, as they should not if species are spatio-temporally localized individuals (Hull 1978, p. 353).

Ignoring all sorts of interesting issues, I shall concentrate on two central points. First, it seems to me that Hull is correct to dismiss statements like "All swans are white" as candidates for being laws of nature. But I think that he offers an incorrect explanation of why such statements are not laws. Second, I claim that he is far too quick to conclude that there are no laws about individual species. When we understand why "All swans are white" isn't a candidate for a law of nature—since it is neither lawlike nor true—we shall be able to recognize the possibility of laws about particular species.

Why isn't "All swans are white" a law? The answer is relatively obvious, given our understanding of the process of evolution: even if it had been true that all members of some swan species—*Cygnus olor*, for example—were white, then this would have been an evolutionary fluke. Organisms flouting the generalization could easily have been produced without any large-scale disruption of the course of nature. A small mutation or chromosomal change could easily modify biosynthetic pathways, and thus result in differently colored plumage. Thus I suggest that "All swans are white" is what it appears to be, a generalization, but a generalization which fails to be lawlike. Biologists are unsurprised when generalizations like this prove to be false, because, given their understanding of the workings of evolution, they would be flabbergasted if there were no exceptions.

In the light of this explanation, we can see what conditions would have to be met for a statement of form "All *S* are *P*", where *S* is a species and *P* a property, to count as a law. Mutations or chromosomal novelties producing the absence of *P* in progeny of members of *S* would have to be so radical that they fell into one of two categories: (a) changes giving rise to inviable zygotes, (b) changes with effects large enough to count as events of instantaneous speciation. In other words, the property *P* would have to be so deeply connected with the genetic constitution of members of the species that alterations of the genome sufficient to lead to the absence of *P* would disrupt the genetic organization, leading to inviable

offspring or to offspring of a new species.⁸ So, *if* there are developmental systems whose modification in certain respects would generate either “hopeful” or “hopeless” monsters, then statements ascribing to members of a species appropriately chosen properties would be candidates for laws about the species. These laws, I suggest, would have the same status as low-level laws of chemistry, generalizations like “DNA molecules contain adenine and thymine molecules in (almost) equal numbers.” While they are more particular than the grand equations of physics, these generalizations are scientifically significant, and are featured in numerous explanations.

So Hull is far too quick to foreclose the possibility of biological laws about particular species. Let me now consider the third main strand in his argument for the idea that species are individuals. What moves Hull is a sense of disanalogy between the set of atoms of an element and a typical biological species. Apparently, atoms of gold might occur anywhere in the universe, while members of *Rattus rattus* are bound to be much more localized. Now, despite the fact that Hull typically formulates the issue by claiming that species are spatio-temporally localized,⁹ the root of his observation is the connectedness of species rather than their boundedness in space-time. The following passage contains the main idea:

If a species evolved which was identical to a species of extinct pterodactyl save origin, it would still be a new distinct species. Darwin

⁸For those who are inclined to believe that the inviability of a zygote because of some genetic disruption does not signal a species boundary, let me suggest a slightly different criterion. One might propose that mutations or chromosomal novelties giving rise to the absence of *P* generate inviable gametes. In this way, the effect of the disruption of the genome is felt at the pre-zygotic stage. (I am grateful to Elliott Sober for bringing to my attention the possibility that an inviable *zygote* may not indicate a species boundary.)

⁹The issue of the spatio-temporal localization of species is a tricky one. (For an illuminating discussion of localizability of the extensions of predicates and the character of natural laws, see John Earman’s 1978.) Given contemporary cosmology, it appears that the extension of ‘atom of gold’, no less than that of ‘organism belonging to *Rattus rattus*’, is spatiotemporally localized (as noted in Kitts and Kitts 1979). Hull’s most explicit discussion of this issue runs as follows: “. . . biological species are spatiotemporally localized in a way in which physical substances and elements are not. No spatio-temporal restrictions are built into the definitions of ‘gold’ and ‘water’” (Hull 1981, pp. 148–9). It seems to me that this response confuses semantical and ontological issues. A defender of the view that species are sets (an ontological view) is free to adopt a number of different theses about how the names of species are defined (or how their referents are fixed). I do not see that remarks about the semantical features of ‘gold’, ‘*Homo sapiens*’, and so forth, cut any ontological ice. We can use proper names (e.g. ‘2’, ‘ π ’) to refer to sets, and it’s possible that our only way of referring to a person (a paradigm individual) should be *via* a description (e.g. ‘the first person to make fire’). Interestingly, Hull immediately proceeds from the passage I have cited to the point about the *connectedness* of species—the point that I regard as central to his case. I see this as reflecting the fact that the official notion of a “spatio-temporally unrestricted class” is unworkable for Hull’s purposes: in one sense, far too many classes are spatio-temporally restricted; in another, the distinction only holds with respect to class *names*.

himself notes, "When a species has once disappeared from the face of the earth, we have reason to believe that the same identical form never reappears. . . ." Darwin presents this point as if it were a contingent state of affairs, when actually it is conceptual. Species are segments of the phylogenetic tree. Once a segment is terminated, it cannot reappear somewhere else in the phylogenetic tree. . . .

If species were actually spatiotemporally unrestricted classes, this state of affairs would be strange. If all atoms with atomic number 79 ceased to exist, gold would cease to exist, although a slot would remain open in the periodic table. Later when atoms with the appropriate atomic number were generated, they would be atoms of gold regardless of their origins. But in the typical case, to *be* a horse one must be *born* of horse. (Hull 1978, p. 349)

Let us say that a set of organisms is *historically connected* just in case any organism belonging to the set is either a member of the initial population included in the set or else an immediate descendant of members of the set. Hull's argument can be reformulated as follows: if species were "spatiotemporally unrestricted classes" then species could be historically disconnected; since no species can be historically disconnected, species are not "spatiotemporally unrestricted classes".

One way to respond would be to concede that species are special kinds of sets (namely historically connected sets). To reply in this way would be to acquiesce in Hull's interpretation of biological practice, but to claim that a different ontological reconstruction of that practice is possible, a reconstruction whose chief merit is that it allows a perspicuous way of raising questions about the internal structure of species taxa. However, this reply grants too much. To be sure, one part of biological inquiry focuses on relations of descent in the phylogenetic nexus. But this is by no means the only type of inquiry with which biologists are concerned, nor should one develop one's approach to the ontology of species in such a way as to foreclose possibilities which are useful in some biological contexts.

More concretely, there are cases in which it would be proper to admit a historically disconnected set as a species. Let me offer an example which is based on an actual event of species formation through hybridization. In the lizard genus *Cnemidophorus*, several unisexual species have arisen through hybridization. In particular, the lizard *Cnemidophorus tesselatus* has resulted from a cross between *C. tigris* and *C. septemvittatus* (Parker and Selander 1976, Parker 1979). Although there are important differences between bisexual and unisexual species, the practice of naturalists and theoretical biologists has been to count *C. tesselatus* as a distinct species, whose status is not impugned by its unisexual character. In fact,

C. tessellatus has served as a test case for comparing genetic diversity in bisexual and unisexual species.

C. tessellatus is probably not historically disconnected. But it might all too easily have been. The actual species probably originated when peripheral populations of the ancestral species came into contact. Clones could even have been established on many different occasions from parental individuals belonging to different breeding populations. A more radical type of discontinuity is also possible. Imagine that the entire initial population of *C. tessellatus* was wiped out and that the species was re-derived after a second incident of hybridization between the two parental species. I claim that this would have been the correct description to give of a sequence of events in which first hybridization was followed by extinction and later by second hybridization. For, supposing that the clones founded in the first hybridization fall within the same range of genetic (morphological, behavioral, ecological) variation present in the population that has persisted to the present, what biological purpose would be served by distinguishing two species? To hypothesize “sibling species” in this case (and in like cases) seems to me not only to multiply species beyond necessity but also to obfuscate all the biological similarities that matter. Hence I conclude that Hull is wrong to chide Darwin for confusing a contingent state of affairs with a conceptual point. In most groups of organisms, historically disconnected species are unlikely—and conceding the logical possibility that *Homo sapiens* might re-evolve after a holocaust does not offer us any genuine comfort. But it is not necessary, and it may not even be true, that all species are historically connected.¹⁰

3. The Troubles of Monism. The traditional thesis that species are sets provides us with a framework within which we can investigate the species category and this framework is not at odds with insights drawn from evolutionary theory. But if species are sets, what kinds of sets are they?¹¹

¹⁰Let me briefly respond to an obvious objection. It may be held that the set-theoretic reformulation of discourse about species—specifically the translation sketched on p. 310 above—grants Hull everything he wants. At this stage, it ought to be clear that this is not so. At least two of the main consequences of the doctrine that species are individuals (the thesis that species are historically connected, and the explanation of the nonexistence of laws about particular species) do not follow from my set-theoretic account. Indeed, I would contend that all of the apparently exciting results which Hull has wanted to establish are not honored by the set-theoretic version. (A more extensive defense of this claim is given in *Species*.)

¹¹There is a short answer: species are natural kinds. I accept this answer, but I don't adopt all the implications some may want to draw from it. In particular, I want to remain agnostic on the issue of whether any species taxon has a non-trivial essence. But what then distinguishes a natural kind? I suggest that natural kinds are the sets that one picks out in giving explanations. They are the sets corresponding to predicates that figure in our explanatory schemes. Are kinds then the extensions of predicates that occur in laws? Pos-

The twentieth century literature in biology is strewn with answers to this question. Most popular has been the so-called biological species concept, developed with great care by Ernst Mayr. According to Mayr's definition, species are "groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1970, p. 12; 1969, p. 26). A somewhat different approach, developed in different ways by G. G. Simpson (1961), Willi Hennig (1966), E. O. Wiley (1981), and others, is to regard the notion of a speciation event as the basic notion and to take a species to be the set of organisms in a lineage (a sequence of ancestral-descendant populations) bounded by successive speciation events.¹² Speciation events themselves can be understood either as events in which a descendant population becomes reproductively isolated from its ancestors (Simpson) or as events in which an ancestral population gives rise to two descendant populations which are reproductively isolated from one another (Wiley and Hennig).¹³ A more radical departure from traditional concepts of species is effected by viewing speciation as a process in which descendant populations are ecologically differentiated from their ancestors (van Valen 1976). And there are still other approaches. In the early 1960s there arose an influential school of taxonomy which proclaimed the virtues of dividing organisms into species by constructing a measure of overall similarity and taking species to be sets of organisms which are clustered by this measure (Sokal and Sneath 1963; Sneath and Sokal 1973). Finally, in the last decade, another taxonomic school, the so-called "pattern cladists" have proposed that a species is a set of organisms distinguished by their common possession of a "minimal evolutionary novelty" (Nelson and Platnick 1981, p. 12; also Rosen 1979 and, perhaps, Eldredge and Cracraft 1980, p. 92).

I do not have space here to explain in detail what these various proposals are, much less to examine their merits. So I shall simply give a

sibly—but not necessarily. The account of explanation I favor (see my 1981) does not require that all explanation involve derivation from laws. One of the central features of that account is that the generality of a scientific explanation need not consist in its using some lawlike premise but in its instantiating a pattern exemplified in numerous other explanations. Hence, though I link natural kinds to the predicates that occur in scientific explanations, I do not require that there be laws about all kinds.

Subsequent discussion in the present paper will not rest on this all-too-brief elaboration of the idea that species are natural kinds. I am grateful to a number of people, most notably Alex Rosenberg, for helping me to see the relation between my own views and the traditional idea of species as natural kinds. A more elaborate account of this relation is undertaken in *Species*.

¹²I should point out that this proposal for demarcating species taxa is the one most congenial to the Hull-Ghiselin thesis. The difficulties that arise for the Simpson-Hennig-Wiley approach provide more reasons to adopt the position defended in Section 2.

¹³Wiley and Hennig diverge from Simpson in disallowing speciation through anagenesis. Wiley, unlike Hennig, is prepared to grant that a species may persist through a speciation event.

brief, dogmatic statement of my main claim and then offer a quick illustration of it. Most of the suggestions that I have mentioned can be motivated by their utility for pursuing a particular type of biological inquiry. But, in each case, the champions of the proposal contend that their species concept can serve the purposes of all biologists. In this I think that they err.

Consider Mayr's biological species concept. There is no doubting the importance of reproductive isolation as a criterion for demarcating certain groups of organisms. To cite a classic example, it was a major achievement to separate six sibling species within the *Anopheles* complex of mosquitoes, and thus to understand the distribution of malarial infection in Europe. (For a classic discussion, see Mayr 1963, pp. 35–7, 1970, pp. 24–5.) This example shows the biological species concept in its native habitat: reproductive isolation is important to recognize when we have organisms with overlapping ranges that are morphologically similar but which do not interbreed.

But it is all too familiar that there are difficult cases. Consider the plight of the paleontologist concerned to understand the rates of evolution in different lineages. Quite evidently, there is no way to evaluate directly some hypothesis about whether two forms, long extinct, were or were not reproductively isolated from one another. Thus conclusions about the succession of species in an evolving lineage must be based upon morphological data. Only the most enthusiastic operationalist would conclude directly from this that the paleontological species concept ought to be morphological. As has been repeatedly pointed out (Hull 1968, Simpson 1961), one can search for correlations between morphological changes and the changes which lead to reproductive isolation, using such correlations to reconstruct the division of the lineage into biological species. However, this response to the operationalist's recommendation misses one important feature of the continued insistence by some paleontologists that the biological species concept will not serve all their purposes. There is a perfectly legitimate paleontological question which focuses on the rates and patterns of morphological diversification within evolving lineages, and paleontologists pursue this question by dividing lineages into species according to morphological changes. To insist that they should always formulate their inquiries by using the biological species concept is to make them take a risky trip around Robin Hood's barn. (For further discussion of this point, see Section 5.)

But paleontology is not the only place in which there are shortcomings of the biological species concept. That concept also fails in application to organisms which do not reproduce themselves sexually. The typical response to that failure reveals a mistake that pervades much traditional thinking about the concept of species.

In an early explanation and defense of the biological species concept, Mayr acknowledged that there is a problem with asexual organisms, but this problem was not to be taken to be particularly threatening.

There is, however, some question as to whether this species definition can also be applied to aberrant cases, such as the mating types of protozoa, the self-fertilizing hermaphrodites, animals with obligatory parthenogenesis, and certain groups of parasites and host specialists. . . . The known number of cases in which the above species definition may be inapplicable is very small, and there seems to be no reason at the present time for “watering” our species concept to include these exceptions. (Mayr 1942, pp. 121–22)

Two interesting features of this passage set the tone for most subsequent defenses of the biological species concept. First, the problem is seen as one of *application*. How do we apply the criterion of reproductive isolation to organisms that do not mate? Second, Mayr attempts to minimize the scope of the problem. Only a few difficult cases are known, and it is suggested hopefully that these may disappear if we learn more about the organisms concerned. The joint effect of these two claims is to portray the biological species concept as a valuable *instrument*. It is recommended to us on the grounds that it will almost always pick out the right groups—as if it were a diagnostic machine that could reveal the patient’s malady in 999 cases out of 1000.

This way of looking at the situation is curious. For it seemed originally that the biological species concept was intended as an *analysis* of previous discourse. For centuries, botanists, zoologists, field naturalists and ordinary people have responded to the diversity of the living world by dividing organisms into species. The biological species concept appeared to offer a reconstruction of their remarks—we were to be given a description of what the species are which would parallel the chemist’s account of what the elements are. But, in Mayr’s response to the problem of asexuality, the goals of the enterprise seem to shift. The biological species concept is no longer seen as identifying the fundamental feature on which organismic diversity rests; it is viewed as a handy device for leading us to the right groups.

Theoretical systematics often seems to presuppose that there is a fundamental feature of organismic diversity, common to all groups of organisms, that taxonomists try to capture by making judgments of the form ‘*A* and *B* are distinct species’. Accounts of the species category propose explanations of what these judgments mean, by offering hypotheses about what the fundamental fact of organismic diversity is. The biological species concept claims that what constitutes the ground of diversity is the

reproductive isolation of groups of populations. Asexual organisms teach us that this cannot be the ground of diversity in all groups of organisms. We can react to this lesson in one of a number of ways. One is to deny that there is any fundamental phenomenon of diversity among asexual organisms, abandoning judgments of form 'A and B are distinct species', in cases where A and B are sets of asexual organisms. But those who work with asexual organisms contend that there are theoretically significant distinctions among such organisms which defy any such radical revision of taxonomic practice. A second response, developed by Mayr, is to count morphological differences as indicators of species distinctness, treating sexual and asexual organisms alike. But this does not touch the real question which theoretical systematics seemed to address. For what we want to know is *what morphological difference is an indicator of*, what we are after when we attend to morphological distinctness.¹⁴ If it is suggested that, in the case of asexual organisms there is nothing more fundamental than morphological difference, that here clustering in morphological space is not evidence of species distinctness but *constitutive* of species distinctness, then we should ask why we fail to attend to this patterning of organismic diversity in the case of sexual organisms as well. Why isn't morphological distinctness *always* constitutive of species distinctness?

It is here that the difficulties of the biological species concept expose an important moral. Although the biological species concept brings out an important pattern in the diversity of nature—the division of organisms into groups that are reproductively isolated from one another is theoretically significant—this is not the only important pattern of organismic diversity. Champions of the biological species concept—and defenders of alternative approaches to the species category—are too quick to assume that problematic groups of organisms can be dismissed as irritating exceptions, or that they can be handled by adding disjuncts to a definition of 'species'. By contrast, I suggest that the problem cases should be taken seriously, in that they point to distinctions among organisms which can be used to generate alternative legitimate conceptions of species. I shall now try to explain why it is to be expected that biology needs a number of different approaches to the division of organisms, a number of different sets of "species".

¹⁴There are some curious twists in recent versions of the biological species concept, including what appears to be a flirtation with essentialism. Consider the following recent statement by Ernst Mayr: "In spite of the variability caused by the genetic uniqueness of every individual, there is a species-specific unity to the genetic program (DNA) of nearly every species". (1982, p. 297) Similar suggestions have been voiced by others (Eldredge and Gould 1972, p. 114), and they reinforce the idea that morphological difference or reproductive isolation are indicators of a more fundamental cleavage among organisms.

4. The Possibility of Pluralism. In the writings of great systematists, there are occasional passages in which the author recognizes the needs of different groups of biologists. Typically, these passages precede the moment at which monism takes over and the writer becomes an advocate for a single conception of species which is to answer to the interests of every one. An excellent example occurs at the beginning of Hennig's classic work on systematics (Hennig 1966, p. 5), where he emphasizes the multiplicity of admissible approaches to classification. Yet, within a few pages (1966, p. 9), Hennig reformulates the question in a way that makes it clear that some one of the systems is to be regarded as privileged, that biology must have a single general reference system.

I shall try to show why it is both desirable and possible to resist the Hennigian move. I begin with an important distinction due to Mayr. Pointing out that biology covers "two largely separate fields", Mayr claims that practitioners in one field ("functional biology") are primarily interested in questions of "proximate causation", while those in the other field ("evolutionary biology") are primarily concerned with issues of "ultimate causation" (1961; see 1976, p. 360). Mayr's choice of terms suggests his own predilections, and threatens his own fundamental insight. There are indeed two kinds of biological investigation that can be carried out relatively independently of one another, neither of which has priority over the other. These kinds of investigation demand different concepts of species. In fact, as I shall suggest, each main type of biological investigation subdivides further into inquiries that are best conducted by taking alternative views of the species category.

The main Mayrian division is easily explained by example. One interesting biological project is to explain the properties of organisms by means of underlying structures and mechanisms. A biologist may be concerned to understand how, in a particular group of bivalve molluscs, the hinge always comes to a particular form. The explanation that is sought will describe the developmental process of hinge formation, tracing the final morphology to a sequence of tissue or cellular interactions, perhaps even identifying the stages in ontogeny at which different genes are expressed. Explanations of this type abound in biology: think of the mechanical accounts of normal (and abnormal) meiosis, of respiration and digestion, of details of physiological functioning in all kinds of plants and animals. For obvious reasons, I shall call these explanations "structural explanations".¹⁵ They contrast with *historical explanations*, accounts that seek

¹⁵In choosing this label, I don't intend to downplay the role of physiological (as opposed to anatomical) considerations. The contrast is between appeals to structure and present function, on the one hand, and appeals to history, on the other. (I am grateful to Marjorie Grene for suggesting to me that my label might mislead.)

to identify the evolutionary forces that have shaped the morphology, behavior, ecology, and distribution, of past and present organisms. So, for example, our imagined biologist—or, more likely, a colleague—may be concerned to understand why the bivalves evolved the form of hinge that they did. Here, what is sought is an evolutionary history that will disclose why the genes regulating the particular hinge morphology became fixed in the group of bivalves.

Neither mode of explanation is more fundamental than the other. If I want to relieve my ignorance about the structures and mechanisms underlying a morphological trait, then I cannot receive enlightenment from an account which tells me (for example) how natural selection favored the emergence of the trait. Equally, I can be well acquainted with the developmental details underlying the presence of a feature and still legitimately wonder why the structures and mechanisms concerned have come to be in place. This is not to deny that structural and historical investigations can prompt further historical and structural inquiries. As we understand more about the structures that underlie facets of morphology or pieces of behavior, new questions arise about the historical processes through which those structures emerged. In similar fashion, deeper understanding of evolutionary history raises new questions about the structures instantiated in the organisms who participated in the historical process. A study of a particular organism can easily give rise to a sequence of questions, some structural and some historical, with structural answers raising new historical questions and historical answers raising new structural questions. 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.

I claim that these two main types of biological inquiry generate different schemes for classifying organisms. Consider the enterprise of structural explanation as it might be developed in microbiological investigations. Our study of viruses initially reveals certain patterns of morphological and physiological similarity and difference: we discover that there are different shapes and constitutions of the viral protein sheaths and that there are differences in the abilities of viruses to replicate on various hosts. These initial discoveries prompt us to ask certain questions: Why does this virus have a protein sheath of this shape? Why is it able to replicate on this host but not on that? Viral genetics proves some answers. We learn that the features that originally interested us depend upon certain properties of the viral genome. At this point our inquiries are transformed. We now regard viruses as grouped not by the superficial patterns that first caught our attention, but by similarities in those properties of the

genome to which we appeal in giving our explanations. Our reclassification may prompt us to differentiate viruses that we would formerly have lumped together, or to regard as mere “variants” organisms previously viewed as of radically different types. But, irrespective of any reforms it may induce, the achievement of an explanatory framework goes hand in hand with a scheme for delineating the “real kinds” in nature.¹⁶

This example mixes science with science fiction. We at present know an enormous amount about the genetics of some viruses, enough to discern minute details of the process of sheath synthesis and even of viral replication. Fiction enters in my suggestion that knowledge of this sort is available across the board, so that we can actually reclassify viruses on the basis of genetic discontinuities. To the best of my knowledge, microbiologists are not currently in a position to apply explicit genetic criteria to demarcate structural species of viruses. Nevertheless, it is not hard to envisage the possibility that future science may operate with a species concept in which microorganisms are divided by particular differences in their genetic material, and in which these differences are regarded as “real” whether or not they correspond to morphological or physiological distinctions, whether or not they coincide with the groupings produced by the evolutionary process.

Consider, by contrast, the enterprise of historical explanation. Again, our inquiries may begin with an unfocused question. We notice a pattern of similarities and differences among certain animals, carnivorous mammals for example, and we ask how this diversity has arisen. Our project may initially be formulated in quite inadequate terms: we may begin by excluding giant pandas (because they are herbivores), hyenas may be classified with cats, marsupials like the Tasmanian “wolf” may be included, and so forth. As we proceed to reconstruct the phylogeny of the carnivores our groupings change, reflecting the recency of common ancestry. We learn to see the “important” similarities (like skull morphology), and to ignore “plastic” traits (like body size). In this way a new classification is produced, which may override similarities in gross morphology, in behavior, in ecology, even, in principle, in genetic structure.

So far I have outlined two main approaches to the classification of organisms, but within each of these more general schemes there are particular variations. Some patterns of organismic diversity may be explained by reference to structural similarities at different levels. When thinking about structural explanation, there is a strong temptation to adopt a reductionist perspective, to hold that the fundamental distinctions among organisms must be made in genetic terms. My example about the viruses

¹⁶Evidently, this scenario recapitulates the views of Putnam and Kripke about the conceptualization of natural kinds. See (Putnam 1975) and (Kripke 1980).

exploits the hold that reductionism exerts on our thinking. Yet we should acknowledge that there may be phenomena whose structural explanation will ultimately be given by appealing to discontinuities in the architecture of chromosomes. (See, for example, White 1978.) Another possibility is that some biological phenomena—like those of phenotypic stability—may be explained by identifying developmental programs, conceived as flow charts that trace cell movements and tissue interactions. (See Figure 1.) So we might arrive at a structural conception of species that identified a species as a set of organisms sharing a common program, without committing ourselves to the idea that there is any genetic similarity that covers exactly those organisms instantiating the program. The situation I envisage is easily understood by taking seriously the metaphor of a *program*. Organisms may be divided into species according to their possession of a common “software”, and this division might cut across the distinctions drawn by attending to genetic “hard wiring”.

At present, we can only speculate about the possibilities for structural concepts of species. A far more detailed case can be made for pluralism about historical species concepts. Let me begin with an obvious point. The enterprise of phylogenetic reconstruction brings home to us the importance of the principle of grouping organisms according to recency of common ancestor. But that principle, by itself, does not legislate a division into kinds. It must be supplemented with a principle of *phylogenetic division*, something that tells us what the important steps in evolution are, what changes are sufficiently large to disrupt phylogenetic connections and to give rise to a new evolutionary unit.

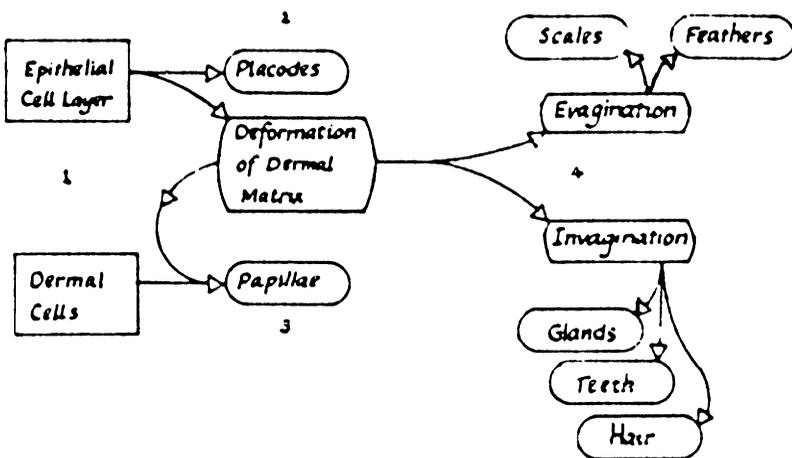


Figure 1. Diagrammatic summary of the skin developmental program (From Oster and Alberch 1982)

There are three main views about the kinds of evolutionary change that break lineages: the production of reproductively isolated branches,¹⁷ the attainment of ecological distinctness, and the development of a new morphology. Each of these principles of division identifies a relationship among organisms that is intrinsically of biological interest. Each can be used to yield an account of the species category in which the units of evolution are taken to correspond to the major types of discontinuity. Alternatively, each can be used in subordination to the principle of grouping organisms according to recency of common ancestor, and this approach generates another three different accounts of species.

Historical species concepts arise from applying two principles. The principle of continuity demands that *a* and *b* be more closely related than *c* and *d* if and only if *a* and *b* have a more recent common ancestor than *c* and *d*. The principle of division, of which there are three versions, takes the general form of specifying the conditions under which *a* and *b* are evolutionarily distinct. The candidate conditions are: (i) *a* and *b* belong to populations that are reproductively isolated from one another, (ii) *a* and *b* belong to different ecological (or adaptive) zones, (iii) *a* and *b* are morphologically distinct. Some currently popular approaches to species give precedence to the principle of continuity, using some favored version of the principle of division to segment lineages. Other conceptions are generated by focusing first on the criterion of division, using common ancestry only as a means of assigning borderline cases (for example, deviant organisms or evolutionary intermediates).¹⁸

This taxonomy of species concepts (Figure 2) already helps us to see how different views of species may be produced by different biological priorities. There are three important types of division among organisms, and each of these three types of division can rightly be viewed as the criterion for disrupting phylogenetic continuity or as a phenomenon of interest in its own right. I have already remarked on the way in which the biological species concept illuminated the issue of the distribution of mosquitoes in the *Anopheles maculipennis* complex. Yet it should be evident that distinction according to reproductive isolation is not always the important criterion. For the ecologist concerned with the interactions

¹⁷I should point out that the criterion of reproductive isolation can itself be applied in two different ways to divide lineages. One can count two stages of a lineage as parts of different species if they are reproductively isolated, or one can view speciation events as occurring only when one species gives rise to descendant populations that coexist and are reproductively isolated from one another. As I argue in *Species*, the first criterion is problematic unless certain theses about the geometry of evolution are true; the second represents the approach of Hennig, Wiley and some other cladists.

¹⁸This type of approach seems to be used by Nelson and Platnick (1981) and by Eldredge and Cracraft (1980). In *Species*, I argue that the use of the concept of a fuzzy set can help in avoiding some difficulties posed by transitional populations.

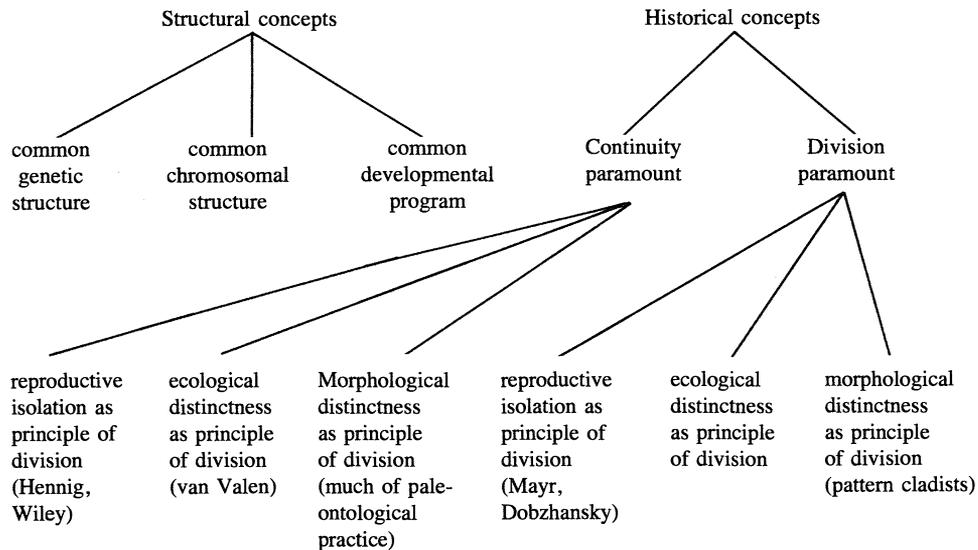


Figure 2

of obligatorily asexual organisms on a coral reef, the important groupings may be those that trace the ways in which ecological requirements can be met in the marine environment and which bring out clearly the patterns of symbiosis and competition. Similarly, paleontologists reconstructing the phylogenies of major classes of organisms will want to attend primarily to considerations of phylogenetic continuity, breaking their lineages into species according to the considerations that seem most pertinent to the organisms under study: reproductive isolation of descendant branches, perhaps, in the case of well-understood vertebrates; ecological or morphological discontinuities, perhaps, in the cases of asexual plants or marine invertebrates. I suggest that when we come to see each of these common biological practices as resulting from a different view about what is important in dividing up the process of evolution we may see all of them as important and legitimate.

Although he did not articulate the point as I have done, Hennig appreciated the diversity of biological interests. Why then did he feel it necessary to demand for biology a single general reference system? Perhaps the most obvious worry about the pluralism that I recommend is that it will engender a return to Babel, a situation in which biological discourse is plunged into confusion. But I think that biology has already been forced to cope with a different case of the same general problem, and that it has done so successfully. One of the lessons of molecular biology is that there is no single natural way to segment DNA into functional units. Present uses of 'gene' sometimes refer to segments whose functional activity affects the phenotype at the level of protein formation, sometimes to segments whose functional activity affects more gross aspects of the phenotype. Even if we pretend that all genes function to produce proteins there is no privileged characterization of genes as functional units.¹⁹ Yet geneticists (and other biologists) manage their investigations quite well, and the use of a plurality of gene concepts does not generate illusions of agreement and disagreement.

This happy state of affairs rests on the following features of the current practice of genetics. (1) For many general discussions about "genes", no particular principle of segmentation of DNA needs to be chosen. The questions that arise can be recast as questions about the *genetic material* without worrying about how that material divides up into natural units. For example, the issue of how genes replicate is reformulated as the question of the mode of replication of the genetic material. *Whatever* view one takes about the segments that constitute genes, the challenge is to

¹⁹For amplification of these points, see my 1982. As Alex Rosenberg has pointed out to me, the increasing complexity of the systems revealed in molecular biology underscores the pluralism about genes defended in that paper.

understand how DNA makes copies of itself. (2) When general inquiries about genes do depend crucially on the segments of DNA identified as genes, it is important for investigators to note explicitly the principle of segmentation that is being used. So, for example, in introducing his thesis about genic selection Richard Dawkins takes pains to identify the units that he will count as genes (Dawkins 1976, p. 34; there is a much more refined discussion of the same point in Dawkins 1982).

The case of the many genes shows how the multiplicity of overlapping natural kinds can be acknowledged without either arbitrary choice or inevitable confusion. Similar resources are available with respect to the species category. Just as there are many ways to divide DNA into "natural functional units", so there are many ways to identify sets of "structurally similar" organisms or to pick out "units of phylogeny". In some discussions of species, what is important to the issue is not dependent on any particular criterion for dividing an evolving lineage into species. When ecologists discuss reproductive strategies, distinguishing between *K*-selected and *r*-selected species, for example, their remarks can be understood independently of any particular proposal for lineage division. Species are conceived as sets of organisms forming part of a lineage, and the distinction at hand is drawn by considering the characteristics of their stages. But in other cases the principle of segmentation is crucial. Paleontologists concerned with comparing species turnover in a group of lineages are likely to misunderstand one another unless they make clear their principle of lineage division.

As Hempel remarked long ago in his celebrated critique of operationalism, the risk of equivocation is ever present in scientific discourse (Hempel 1954; 1965, pp. 126–7; 1966, pp. 92–7). To guard against confusion it is futile to attempt to fashion some perfectly unambiguous language. Instead, responsible scientists should recognize where dangerous ambiguities are likely to occur and should be prepared to forestall misunderstandings. Biologists have already learned to be responsible in discussions of genes. The same responsibility can be attained in the case of species. To allow pluralism about species and to deny the need for a "general reference system" in biology is not to unlock the doors of Babel.²⁰

²⁰Thus there is no univocal answer to the question of how to describe the type of hypothetical situation beloved of philosophers. Suppose we have a species *S* and discover the existence of a historically unrelated group of organisms that agree with the members of *S* in any respect we choose (reproductively compatible, genetically similar, and so forth). Does the group count as a subset of *S*? I claim that the answer must be relative to a *prior decision* on whether or not to employ a historical species concept. Use of such a concept is not forced on us, and it may prove helpful in seeing this to consider a range of organisms and a range of biological investigations. What we may be inclined to say when *S* is *Rattus rattus* may well be different from what we say when *S* is the bacteriophage *T₄*. (I am grateful to Jonathan Bennett for prodding me into making this point explicit.)

5. Three Consequences. I have tried to outline and to motivate a general approach to the category of species. I want to conclude by drawing three morals, one for an area of current biological dispute, one for a question in the philosophy of science, and one which overlaps biology and philosophy. I shall begin with the biological issue.

Paleontologists are currently divided on a number of important issues about the tempo and mode of evolution. In an important and much discussed contribution to these debates, Peter Williamson (1981) provides extensive documentation of the fossil record of several mollusc lineages from the Lake Turkana Basin. Williamson's data (see Fig. 3) reveal ab-

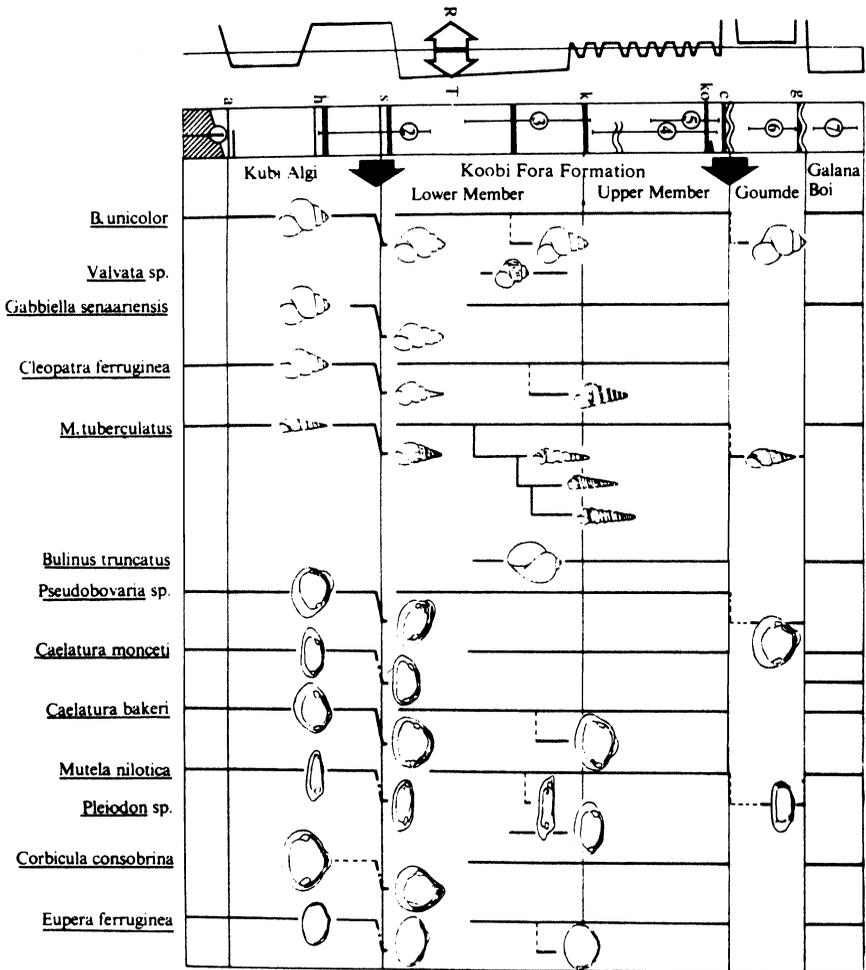


Figure 3. The pattern of morphological change in some molluscs from the Turkana basin (From Williamson 1981).

rupt changes in phenotype punctuating periods of phenotypic stasis. Moreover, the episodes of phenotypic change are themselves associated with an increase in phenotypic variability. Williamson draws attention to this association, and goes on to make some speculations about the genetics of speciation (1981, pp. 442–3).

There are two important ways in which Williamson's data may be interpreted. The first is to suppose that Williamson is employing Mayr's biological species concept, and that he intends to study transitions between biological species. When we choose this reading certain questions about the data become relevant. In particular, we have to ask if the species boundaries identified on the basis of phenotypic considerations coincide with the attainment of reproductive isolation.²¹ Thus one contribution that the essay makes is towards advancing our understanding of speciation, *conceived as a process in which descendant populations achieve reproductive isolation from a persisting ancestral population*. If Williamson's findings are interpreted in this way, they bear on *one* issue of the tempo of evolutionary change and *one* issue of the genetics of speciation. Is the attainment of reproductive isolation a process that occurs rapidly, punctuating long periods of stasis? What mechanisms of population genetics underlie this process?

The second construal ignores any considerations about reproductive isolation. Williamson's data reveal a pattern of phenotypic change, and we can concentrate on this pattern without linking it to claims about reproductive isolation. If processes of speciation are simply identified with the rapid morphological transitions that Williamson describes, then we can inquire about the tempo of these processes and about their underlying genetic basis. Nor are these uninteresting questions. It is no less significant to ask after the tempo and mode of speciation, *conceived as a process of morphological discontinuity*, than it is to inquire about the attainment of reproductive isolation. Williamson's suggestions about genetic mechanisms can be construed as hypotheses about the genetic changes that underlie those episodes of phenotypic modification (with increased phenotypic variability) which are recorded in his data. We do not need to introduce the idea that these episodes lead to reproductive isolation.

Williamson has sometimes been criticized on the grounds that his morphological findings do not rule out the possibility of cryptic "speciation events" during periods of alleged stasis. (Schopf 1981 makes a similar point against claims of documentation of punctuated equilibrium.) Whether or not these criticisms succeed against the first interpretation, they are

²¹There are complications here. One of the lineages (*Melanoides tuberculata*) is asexual. Hence, Williamson's claim must be that the morphological discontinuities correspond to the lineage divisions marked out by reproductive isolation—*where demarcation by reproductive isolation is possible*. This example underscores the point made in Section 3.

plainly irrelevant to the second. The pattern of phenotypic change, a pattern which the fossil record wears on its face, can itself serve as the basis for some important inquiries about the tempo and mode of evolution. By separating different conceptions of species and of speciation, we can disentangle different important issues that arise in biology, and recognize the significance of investigating a number of different patterns in the diversity of life.

At this point let me take up the question that is common to philosophy and biology, the question of the "reality" of species. It is important to understand that realism about species is quite independent of the view that species are individuals. Notice first that if realism about species is construed as the bare claim that species exist independently of human cognizance of them, then anyone who accepts a modest realism about sets can endorse realism about species. Organisms exist and so do sets of those organisms. The particular sets of organisms that are species exist independently of human cognition. So realism about species is trivially true.

To make realism come so cheap is obviously not to recognize what provokes biologists and philosophers to wave banners for the objectivity of systematics. (See Sober 1980 for a clear elaboration of this point.) What is at issue here is whether the division of organisms into species corresponds to something in the *objective structure* of nature. Articulating this realist claim is difficult. But I suggest that however it is developed, it will prove compatible with pluralism about species. *Pluralistic* realism rests on the idea that our objective interests may be diverse, that we may be objectively correct in pursuing biological inquiries which demand different forms of explanation, so that the patterning of nature generated in different areas of biology may cross-classify the constituents of nature. (There are suggestions about how to articulate this point in Boyd 1979 and in my own 1982.) Despite the fact that realist theses about the objectivity of classifications cry out for analysis, we can recognize the plausibility of those theses when we reflect on Williamson's molluscs. Williamson's lineages should remind us that there are a number of objective patterns of evolutionary change. The pluralistic realist is someone who is concerned to understand all of them.

Finally, let me turn to the moral for philosophy of science. In thinking about the general problem of conceptual change in science, we are inclined to consider two main possibilities. With the advantage of hindsight, we see that our predecessors were referring to natural groups of things, about which they may have had radically false beliefs. Or, perhaps, we view them as referring to sets that cut across the natural kinds in bizarre ways. The example of the concept of species—and, I would suggest, that of the concept of gene (1982)—reveals an intermediate sit-

uation. Here we find ourselves unable to provide some short description that will finally reveal the natural group that our predecessors struggled to characterize, but neither are we willing to dismiss them as simply producing an uninteresting heterogeneous collection. The set of species taxa is heterogeneous, but it is not wrongheaded in the way that some early attempts at chemical classification are.

If I am right, then there will be no simple description that will pick out exactly those sets of organisms which some biologists reasonably identify as species taxa. We shall not be able to reconstruct the language of biology and to trace its historical development in the way in which we have been able to cope with cases of conceptual change in chemistry. But this does not mean that we are swept into the cynic's view of species. For although it may be true that species are just those sets of organisms recognized as species by competent taxonomists, there is a way to understand why just those sets have been picked out. That way is not the familiar way of using current theory as an Archimedean point from which we can, at last, provide a single descriptive characterization of the groups to which our benighted predecessors have referred. Instead, we must recognize that there are many different contexts of investigation in which the concept of species is employed, and that the currently favored set of species taxa has emerged through a history in which different groups of organisms have been classified by biologists working on different biological problems. The species category can be partitioned into sets, each of which is a subset of some category of kinds. We can conceive of it as generated in the following way. A number of biologists, $B_1 . . . , B_n$, each with a different focus of interest, investigate parts of the natural world. For each B_i there is a subset of the totality of organisms, O_i , which are investigated. B_i identifies a set of kinds, K_i , the kinds appropriate to her interest—that partition O_i . The set of species taxa bequeathed to us is the union of the K_i . In areas where the O_i overlap, of course, there may be fierce debate. My suggestion is that we recognize the legitimacy of all those natural partitions of the organic world of which at least one of the K_i is a part.

This schematic account of the set of species taxa we have inherited is intended to make clear the moral of my story. To appreciate the rationale for the species category we must reconstruct the history of our discourse about species, and there is no quick substitute for that reconstruction. The cynic's definition may be the beginning of wisdom about species. But it is only the beginning.

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³ **A Radical Solution to the Species Problem**

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³ **Are Species Really Individuals?**

David L. Hull

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