

PART V

SPECIES

INTRODUCTION TO PART V

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The species concept must serve two goals in biology—as a fundamental unit in evolution and a fundamental unit of classification. In biological evolution species are the things that evolve, that split successively through time to form the phylogenetic tree. Species are also one level in the taxonomic hierarchy. Organisms are grouped into species, species into genera, genera into families, and so on. Considerable unification can be brought about in biology if the basic units of classification can be made to coincide with the basic units of evolution, assuming something like 'basic units' exist. One assumption that pervades discussions of the species problem is that a single level of organization exists across all organisms, that can be properly termed the 'species level'. The goal is to discover this level and the mechanisms that produce it.

As is usually the case when a single entity must serve two or more functions, tensions arise. Evolutionary biologists are interested in finding out how the evolutionary process works. They investigate such problems as how much gene flow among various populations of the same species is necessary to keep all these populations integrated into the same species, how frequent interspecific hybridization actually is, and the effects of geographic isolation on species. Systematists are interested in recognizing species, diagnosing them, and ordering them in a taxonomic hierarchy. Stability is an important desideratum for them, because the groupings that they produce are to be used by *all* biologists, not just evolutionary biologists. De Queiroz and Donoghue (Ch. 15) show the difficulties that arise when a criterion used traditionally for higher taxa (monophyly) is extended to the species category.

From Darwin on, various systematists have resisted the identification of the basic units of evolution with the basic units of classification. One school can be called 'idealists', for want of a better term. They view species in the same atemporal way as physicists view the physical elements. They want to order living species according to something like the periodic table. For

idealists species are as atemporal as gold. All atoms with the atomic number 79 are atoms of gold, regardless of place, time, origin, or condition. Biological species also seem to exhibit certain timeless relations. The goal is to find the key that can individuate and order species the way that atomic number orders the physical elements (for a present-day example of this school, see Webster and Goodwin 1996).

Evolutionary biologists want to understand the evolutionary process. If species turn out to be very cryptic and variable, integrated by a variety of mechanisms, then so be it. Systematists feel a stronger need for their species concept to be applicable than do evolutionary biologists. They must produce classifications that biologists—all biologists—can use in their work, even if this order is an over-simplification from an evolutionary perspective. For a species concept to be applicable, species must be recognizable in nature. Thus, systematists by necessity are interested in epistemological issues: for example, how we are to recognize a species as a species.

Thirty years or so ago, a school of systematists (numerical pheneticists) arose that put recognition first. Species are just one level of a hierarchy ordered according to degree of similarity. Species are groups of organisms exhibiting X amount of similarity, genera are more inclusive groups of organisms exhibiting Y amount of similarity, and so on. For them, phylogenetic descent is irrelevant. Sessile organisms with sessile propagules living in Patagonia and Norway would belong to the same species if they exhibit the same degree of morphological similarity. Their isolation from each other would pose no problems whatsoever. As strong as the desire is to make systematics as operational as possible, most systematists are willing to take on the more ambitious task of discerning species as the things that evolve.

A third issue that has arisen in the context of controversies over species is their ontological status. What sorts of things are species? A distinction that has characterized Western thought since its beginnings in ancient Greece is between individuals and classes, and the classic example of this distinction is between an individual organism (such as Gargantua) and the species to which it belongs (*Gorilla gorilla*). Gargantua was born at a particular place and time, grew to adulthood, and eventually died. His name simply denoted him. Just because he was named 'Gargantua', he need not be an especially large gorilla. Species and all higher taxa are quite a different sort of thing. They are classes whose names can be defined by a list of characters. Classes can be defined in spatio-temporal terms so that they are located at particular times and places—for example, all the gold bars in Fort Knox. But classes are important because they can be general.

The classes that are important in science are those that are spatio-temporally unrestricted, so that they can function in laws of nature.

Discovering new physical elements has always been considered an important event in physics. The physical elements are part of the warp and woof of nature. In the golden years of systematics, discovering new species was also treated with some respect, especially if these species were gigantic, exotic, or closely related to *Homo sapiens*. However, after Darwin, systematists were forced to acknowledge that the number of species, past and present, is huge. Millions upon millions of species have evolved and gone extinct. Millions more will do the same in the future. If statements of the traits that characterize each of these millions upon millions of species are considered laws of nature, this notion becomes trivialized beyond redemption. No one is going to be awarded a Nobel Prize for discovering yet another species of fruit-fly.

Throughout the history of systematics, even before the advent of the concept of evolution, biologists have thought that species are in some sense 'special'. They do not represent just a certain level of similarity. Perhaps higher taxa are not 'real', but species are. First Ghiselin (1974), then Hull (1976), explained this feeling that species are different from higher taxa in terms of their being more closely akin to individuals than to classes. Like all individuals, they have a beginning and ending in time, a certain location (commonly termed the 'range' of the species), and exhibit various degrees and sorts of integration. Species are the entities over which biological laws operate.

As this distinction was exposed to intense scrutiny, systematists and evolutionary biologists have concluded that the sharp distinction between individuals and classes is too simple. Species are clearly not classes, unless 'class' is defined so broadly that everything from a bare particular to Richard Nixon becomes a class (or a set). Species are more like individuals, but individuals come in a variety of kinds. One of the topics in the recent literature on the species problem concerns the sorts of integration and cohesiveness that characterize biological species. Does a single level of integration and cohesiveness exist across all organisms, from single-celled to multi-cellular organisms, from sexual to asexual organisms, from plants and protists to animals?

As with the topics treated in earlier parts of this anthology (e.g. Parts III and IV), the issue of pluralism has entered into discussions of the species problem. Each side attempts to define the other as holding extremely radical views. Monists complain that pluralists have provided no principled reasons to limit the luxuriant growth of alternative perspectives and explanations. Species are anything that anyone chooses to make them, from the

eternal and immutable species of Aristotelian philosophy to the operational taxonomic units of the numerical pheneticists or even the divinely created species of the Creationists! Pluralists, in their turn, complain that monists think that nature can be divided up in one and only one way. More than this, each monistic kind must be definable by a single criterion. For example, Kitcher (1993; reproduced above as Chapter 12) considers his unitary analysis of 'function' in terms of design 'pluralist', because two sorts of design can be found in nature.

Actually, both pluralism and monism are needed in science—the generation of new hypotheses and their critical winnowing. Sometimes scientists in a particular area get locked so firmly into a single way of viewing the world that they find it impossible to generate new solutions to unsolved problems. In such circumstances, calls for pluralism are warranted. However, sometimes scientists in a particular area are inundated with alternative explanatory schemas. Every phenomenon can be explained in myriad ways. In such circumstances a strong dose of monism can't hurt. Such a heuristic interpretation of the continuing dispute between monists and pluralists, however, is not likely to satisfy more metaphysically inclined philosophers (for general discussions, see Dupré 1993, Rosenberg 1994, and Ereshefsky 1992, reproduced here as Ch. 16).

In this connection, Mishler and Brandon (1987; reproduced here as Ch. 14) distinguish between grouping and ranking. Certain criteria are used to decide which organisms go together in the same species. For example, numerical pheneticists provide a list of characteristics for each group of organisms. Any organisms that have enough of these characteristics (are similar enough to each other) belong to the same species. In addition, numerical pheneticists define ranks by decreasing degrees of overall similarity—how similar is similar enough? A high degree of similarity is required for species, a lesser degree for genera, and so on. Mishler and Brandon, to the contrary, argue for a species definition that is monistic with respect to its grouping criterion (monophyly) and pluralistic with respect to its ranking criteria. Current debates over the species category turn on disagreements about which characteristics are to be used for grouping and which for ranking.

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INDIVIDUALITY, PLURALISM, AND THE PHYLOGENETIC SPECIES CONCEPT

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INTRODUCTION

The species question continues to be of central interest to biologists and philosophers. Perhaps surprisingly for a topic that has been discussed so frequently for so long, new insights and original interpretations continue to emerge. In our opinion, however, widespread confusion remains on several important points. Our purpose here cannot be to provide a general review of the subject (for which see Mayr 1982, 1987). We wish instead to concentrate on the flurry of recent philosophically oriented papers on species (Bernier 1984; Ghiselin 1987; Haffer 1986; Holsinger 1984, 1987; Hull 1984, 1987; Kitcher 1984a, b; Kitts 1983, 1984; Mayr 1987; Rieppel 1986; Ruse 1987; Sober 1984; Williams 1985), and to make several points. First, the distinction between individuals and classes is an over-simplification; at least four important subparts of the concept of individuality can be recognized. Second, a phylogenetic species concept has recently been elaborated that can simultaneously and rigorously meet the needs of systematists and evolutionary biologists. Species delimited in this way will never be classes, yet they will often not be fully individuals either. Third, in order to apply this concept, the usually unrecognized distinction between 'grouping' and 'ranking' components of a species concept must be realized, and the appropriate meanings of 'pluralism' and 'monophyly' with respect to species must be appreciated.

INDIVIDUALITY

The 'radical solution to the species problem' advocated by Ghiselin (1974) and Hull (1976) was to consider species as individuals rather than as

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classes. By 'individuals' they meant entities that are 'spatiotemporally localized, well-organized, cohesive at any one time, and continuous through time' (Hull 1987: 168). This idea has been enormously productive as a source of new insights into the species problem. Nevertheless, it is time to move beyond the simple class-individual distinction to a more detailed consideration of properties held by biological entities.¹

A number of authors have suggested that the class-individual distinction advocated by Ghiselin and Hull is over-simplified, and have suggested other ontological categories (Wiley 1980, Mayr 1987). Indeed, Hull (1976) himself suggested that a species may fall into some hybrid category that is neither an individual nor a class; but, he claimed, it is at least clear that species are not classes. The last conclusion we find ourselves in complete agreement with. It has been established beyond a doubt, in our opinion, that neither species nor other biological taxa can productively be viewed as sets or classes defined by possession of certain features. We believe that it is possible to define classes that are coextensive with particular biological species (see attempts by Kitcher (1984b)). But such definitions do not add anything to the theoretical insights that have been gained by the 'species as individual' concept.

A refinement that can lead to further theoretical insights is to unpack the concept of individuality into important sub-parts. With regard to evolutionary biology, at least four major sub-concepts of individuality can be recognized. We are not concerned with what sub-concept (or combination thereof) should be called true individuality. Rather, we will argue that various kinds of biological entities (including those called 'species' by systematists) will meet various combinations of these criteria of individuality, and that it is necessary to distinguish among them. Our concern is to argue against the largely tacit assumption that entities meeting some of these criteria will meet them all.

We have suggested names for these sub-concepts, based on terms that have been used in the literature; other terminologies are clearly possible. It is important to note that the first two of these sub-concepts are different in kind from the second two. The former refer to 'patterns'—that is, effects of biological processes—and the latter refer directly to the action of processes. We particularly use species taxa as currently defined for examples

¹ We should note at the outset that, contrary to the impression one is likely to get from the literature on species-as-individuals, the class-individual distinction is not a distinction taken directly from logic. First, Hull and Ghiselin are using a restricted notion of classes. Something counts as a class for them only if its membership can be specified in a spatio-temporally unrestricted way. Logic places no such restriction on classes. Although Hull (1978) is reasonably clear on this point, not everyone else has been, and this has led to some confusion. Second, the operative notion of 'individual' comes more from common-sense zoology than from logic.

here, but will defer our recommendations for proper application of these ideas to species until a later section.

Spatial Boundaries

One important aspect of individuality is the spatial localization of a particular entity. The traditional view of a class is that its members may be present anywhere in the universe if the proper defining features are present. All known evolutionary processes, however, certainly produce entities at all taxonomic levels that are spatially restricted. Thus it would seem that species taxa, properly named, would always meet this criterion.

Temporal Boundaries

A second important aspect of individuality involves temporal restriction of an entity. A taxon must have a single beginning and potentially have a single end in order to count as an individual under this criterion. Thus, such taxa may not re-originate, even if the second-arising entity is indistinguishable from the first. It should be clear that this criterion can be decoupled from the first. Depending on one's definition of species, taxa could easily be recognized that are spatially, but not temporally, restricted. One example would be repeated polyploid speciation in plants via hybridization (Holsinger 1987). The currently controversial systematic concept of monophyly is relevant here, but we defer discussion until a later section.

Integration

Two very different types of causal interaction between processes and biological entities have been lumped under the concept of individuality, thereby causing confusion. We will argue that these types of causal interactions can be, and often are, disconnected from each other and/or from the resulting patterns discussed above; thus careful distinctions must be made.

We have designated 'integration' to refer to active interaction among parts of an entity. In other words, does the presence or activity of one part of an entity matter to another part? Examples of this type of causal interaction include the effect of the heartbeat on the circulatory system of an animal, mating relationships and gene flow within populations and species, and processes of frequency-dependent and density-dependent natural selection. It has been argued by a number of authors (summarized

by Mishler and Donoghue 1982) that species taxa as currently delimited often do not meet this criterion of individuality (even though they may meet one or both of the two criteria listed above).

Cohesion

We have designated 'cohesion' to refer to situations where an entity behaves as a whole with respect to some process. In such a situation, the presence or activity of one part of an entity need not directly affect another, yet all parts of the entity respond uniformly to some specific process (although details of the actual response in different parts of the entity may be different because of the operation of other processes). Examples of this type of causal interaction include the failure of a corporation due to a stock-market crash, developmental canalization in biological systems, and processes of density-independent natural selection. Clearly, species taxa as currently delimited may show cohesion as defined in this way, or integration, or both, or neither.

Problems with Application of Individuality to Species

It should be clear from the above examples that, despite its philosophical appeal, the 'species as individual' concept developed by Ghiselin and Hull cannot be applied in its simplistic form to most species taxa as currently delimited; nor, we would argue, could taxonomic practice be revamped so as to make it generally applicable (see Mishler and Donoghue 1982 for further arguments and examples). The major reasons for this inapplicability are two: the plethora of causal processes acting on biological entities and the lack of correspondence between either these processes or patterns resulting from them.

As pointed out by Van Valen (1982) and Holsinger (1984) among others, a great number of processes impinge on organisms and groups of organisms. A non-exhaustive list would include breeding relationships, competition, geological change, developmental canalization, symbioses, and predation. Entities can simultaneously behave as individuals with respect to different processes, at different levels of inclusiveness (Holsinger 1984). Furthermore, groups of organisms defined by aspects of individuality with respect to one process are often not congruent with groups defined with respect to a second process (Mishler and Donoghue 1982).

Mary Williams's recent attempt (1985) to link her concept of 'Darwinian subclan' with Ghiselin and Hull's formulation of species as individuals fails

for both of these reasons. Her whole argument rests on the assumption that all biological species are in the domain of a legitimate interpretation of 'Darwinian subclan', or in other words, that species are Darwinian subclans. However, this amounts to the assumption that species are cohesive units with respect to (at least some) selective forces—that is, that organisms within a species are all acted upon by those same forces. This flies in the face of much of what is known about selection. For example, a species ranging over a geographical cline would hardly qualify as a Darwinian subclan. For a more theoretical example, consider the intrademic models of kin and group selection (Wilson 1980). Here the population units that are cohesive with respect to selection are generally much smaller than the local population, much less the entire species. It is possible, even likely, that species will be Darwinian subclans for some period of their existence (especially at their origin), but this does not help Williams's argument. She needs this to be generally true. However, current knowledge of evolutionary processes does not back her up.

The upshot is that species taxa often are not integrated or cohesive because of particular selective regimes. Other processes causing integration and/or cohesion of species taxa include gene flow and developmental canalization (Van Valen 1982, Mishler 1985). As mentioned above, species taxa as currently recognized may not be integrated or cohesive in any sense (although, as will be discussed below, this situation might be changed by revision of taxonomic practice). Furthermore, there is no reason to believe that reproductive processes and selective processes pick out the same units in nature (Mishler and Donoghue 1982, Holsinger 1984)—a correspondence necessary to relate Williams's Darwinian subclans to Mayr's biological species concept.

To summarize this section, it is useful to consider the nature of various examples of biological entities with differing degrees and aspects of individuality, to drive home the point that application of the simple dichotomy between individuals and classes has obscured important distinctions. Are there important biological groupings that are spatio-temporally localized but neither integrated nor cohesive? Yes, monophyletic higher taxa, called 'historical entities' by Wiley (1980), and Darwinian clans, as formalized by Williams (1970), would usually fit such a description. Mayr (1987) suggests that species often represent an intermediate kind of entity (which he terms a 'population') that have spatio-temporal localization but weak integration and cohesion. Thus the distinction made above can admit to differing degrees of integration or cohesion, ranging from strong (in a paradigmatic individual organism) to weak or absent.

Are there important biological groupings that are integrated and/or

cohesive but not spatio-temporally localized? Yes, groups defined by their participation in processes, such as plant communities, pollinator guilds, trophic levels, mixed-species feeding flocks, or C_4 photosynthesizers, may be highly integrated, cohesive, or both, and yet lack any temporal boundaries. Further examples are given by polyphyletic or paraphyletic taxonomic groupings. Such groups may be cohesive because of ecological factors or shared developmental programmes, but lack a unique beginning (in the case of polyphyletic groups) or a unique end (in the case of both kinds of groups). Integration and cohesion do seem to require some form of spatio-temporal connectedness, but, as our examples illustrate, this does not imply temporal boundaries. Does it strictly imply spatial boundaries? We think it does; in any case we cannot think of any plausible examples of integrated and/or cohesive entities lacking spatial boundaries.

THE PHYLOGENETIC SPECIES CONCEPT

The search for a satisfactory concept of species is complicated by the need to simultaneously reconcile recent advances in evolutionary theory with recent advances in systematic theory, with empirical requirements of objectivity and testability, and with constraints imposed by the formal Linnaean nomenclatorial system. Before discussing one recently proposed solution, there is a need to introduce and clarify two important subjects: pluralism and the distinction between grouping and ranking.

Pluralism

As a number of authors have pointed out, controversies in evolutionary biology over causal agents generally do not involve claims that all but one favoured agent are impossible. Rather, a number of causal agents are acknowledged to be possible, and controversy centres around which agent is the 'most important' (Gould and Lewontin 1979, Beatty 1985).

The result of this situation in evolutionary biology has been a number of calls for 'pluralism', meaning generally to keep an open mind about which particular causal agent is to be invoked as an organizing principle in any particular case. The case of species concepts has heard similar calls (Mishler and Donoghue 1982, Kitcher 1984a, b).

However, in the case of species, two very different sorts of 'pluralism' have been advocated; thus confusion has resulted. Both sorts of pluralism are based on the fact that many different (and non-overlapping) groups of organisms are functioning in important biological processes (see discussion

by Holsinger (1984, 1987)). Both sorts of pluralism deny that a universal species concept exists. However, they differ in their application to particular biological cases. Kitcher's (1984a, b) brand of pluralism implies that there are many possible and permissible species classifications for a given situation (say the *Drosophila melanogaster* complex), depending on the needs and interests of particular systematists. In contrast, Mishler and Donoghue's (1982) brand of pluralism implies that a single, optimal, general-purpose classification exists for each particular situation, but that the criteria applied in each situation may well be different. This latter meaning of pluralism, we would argue, is close to the use of the term by Gould and Lewontin (1979). Furthermore, we would also argue that its use results in perfectly reasonable and rigorous scientific solutions to particular problems. The only caveat is that problems (such as difficult species complexes) that seem at least superficially similar may require different criteria for solution.

Ghiselin (1987) has unfortunately confused these two uses of 'pluralism' and tarred them both with a broad brush. Also unfortunately, he has engaged in *ad hominem* attacks (by suggesting that pluralists are lazy, incompetent, dishonest, and generally not engaged in science at all) and fallacious arguments. Despite his unsupported assertion that the biological species definition is 'fully applicable to plants', numerous botanists (and others) have published careful empirical and theoretical analyses of the difficulties with applying the biological species concept (see Mishler and Donoghue 1982 for references). Problems having to do with lack of correspondence between patterns resulting from different causal processes, and the gradual nature of breeding discontinuities in plants, cannot be waved aside casually.

To further distinguish between the two meanings of 'pluralism' and to clarify the proper usage of the term with respect to biological theories, it is necessary to examine connections with the concept of parsimony. It is natural and correct for scientists to have a bias towards monism, because of the fundamental scientific tenet of economy in hypotheses. Hull's (1987) arguments for consistency in using cessation of gene flow as a uniform definition of the species category carry a lot of weight (see also arguments by Sober (1984)). The burden of proof rests squarely on someone who argues that the current domain of explanation of a monistic theoretical concept must be broken into smaller domains, each with its own explanatory concept. Note that this sort of pluralism (which is the sort advocated by Gould and Lewontin (1979) and Mishler and Donoghue (1982)) is 'pluralistic' only during the transition as a prevailing monistic concept is broken up. Once controversy settles and the transition is complete, you are

left with a greater number of explanatory concepts, each quite monistic within its proper domain. Parsimony considerations weigh in balance against the need to provide proper explanations for biological diversity. As scientists, we strongly attempt to minimize the number of theoretical concepts (to one if possible) allowed to delimit (for example) basic taxonomic units. Yet we should grudgingly grant status to additional concepts if the need for them is proved in particular cases.

This use of pluralism is clearly not the use advocated by Kitcher (1984a, b). He implies a sort of 'permanent pluralism', where an indefinitely large number of theoretical concepts (limited only by interests of particular biologists) remain acceptable within a single domain. We share the scepticism of Sober (1984), Hull (1987), and Ghiselin (1987) towards this meaning of pluralism. Its use with respect to species concepts would seem to rob systematics of any objective way of choosing between conflicting classifications or of any use of species as units of comparison. Therefore, in what follows, we use 'pluralism' in the sense of Mishler and Donoghue (1982).

Grouping versus Ranking

All species concepts must have two components: one to provide criteria for placing organisms together into a taxon ('grouping') and another to decide the cut-off point at which the taxon is designated a species ('ranking'). This distinction (as detailed by Mishler and Donoghue (1982), Donoghue (1985), and Mishler (1985)) has often not been recognized (but see a similar distinction made by Mayr 1982: 254). Taking the biological species concept as an example, its grouping component is 'organisms that interbreed'. But since such groups are found at many levels of inclusiveness, especially if 'potentially interbreeding' is added to the grouping criterion, a ranking component is needed which usually is something like 'the largest grouping in which effective interbreeding occurs in nature'.²

Since both components are implicit in any adequate species concept, confusion is likely to result if the distinction between them is ignored. Thus Hull's (1987) argument that using patterns of gene flow to define species will result in 'a consistently genealogical perspective' is unsound. It depends on whether reproductive criteria are used for grouping or for

² As pointed out by Hull (personal communication), when the distinction between grouping and ranking has previously been made, it was often blurred. This may often be because researchers use variations on the same theme for both grouping and ranking: e.g. patterns of morphological similarity or of gene exchange. As will be apparent below, we advocate distinctly different criteria for grouping than for ranking.

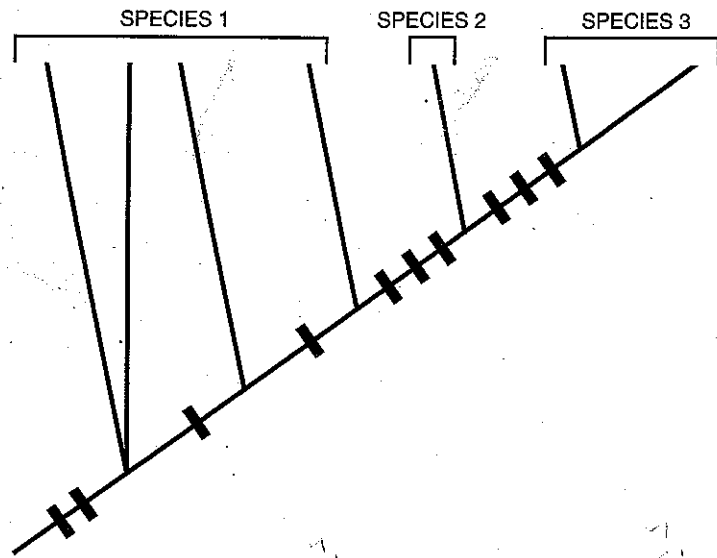


FIG. 14.1. A hypothetical cladogram showing three named species. Synapomorphies are shown as cross-bars; autapomorphies are not shown. Species 1 is paraphyletic.

ranking. Both Rosen (1979) and Donoghue (1985), among others, have nicely shown that the use of reproductive criteria in grouping can easily result in non-monophyletic taxa, in contrast to the genealogical units Hull (along with us) hopes for. The 'recognition concept of species' (Paterson 1985), wherein species are defined by the possession of a common fertilization system, suffers from a similar problem, in that non-monophyletic taxa often result (see Fig. 14.1, where species 1 may well be definable by reproductive criteria, but is not monophyletic).

Further objections to various prevailing species concepts have been given by Mishler and Donoghue (1982), Donoghue (1985), and Mishler (1985). These authors made the following points. (1) None of the dozens of species concepts held currently by various authors can provide grouping criteria able to produce truly genealogical species classifications (including, curiously enough, species concepts advocated by cladists, a group dedicated to genealogical classification). (2) In order to reflect the diversity of causal agents directing evolutionary differentiation in different lineages, no universal ranking criterion can be found.

what does this mean? an organism as a single individual organism? (see 8/21)

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An alternative perspective on species as genealogical, theoretically significant taxa has been developed by Mishler and Donoghue (1982), Donoghue (1985), and Mishler (1985), and called the 'phylogenetic species concept' (not to be confused with the concept proposed by Cracraft (1983), with the same name). This concept explicitly recognizes a grouping and a ranking component, is monistic with respect to grouping, yet pluralistic (in the sense advocated above) with respect to ranking, and produces species taxa with at least some aspects of individuality.

The grouping criterion advocated by Mishler and Donoghue is monophyly in the cladistic sense. Further discussion of the meaning of 'monophyly' is needed (see below), because the term is not normally applied to species in a substantive way by cladists. For now it suffices to say that 'monophyly' here is taken to refer to a grouping that had a single origin and contains (as far as can be empirically determined) all descendants of that origin.

Monophyletic groupings as roughly defined above exist at all levels of inclusiveness; thus a ranking criterion for species is needed as the basal systematic taxon (i.e. the least inclusive monophyletic group recognized in a particular classification). It is here that Mishler and Donoghue have advocated a pluralistic adjustment in the number of ranking criteria allowable for consideration in particular cases. They argued that the currently favoured monistic ranking concept of absolute reproductive isolation is not the most appropriate for all groups of organisms. The ranking concept to be used in each case should be based on the causal agent judged to be most important in producing and maintaining distinct lineages in the group in question. The presence of breeding barriers might be used, but so might selective constraints or the action of strong developmental canalization (Mishler 1985). In the great majority of cases, little to nothing is actually known about any of these biological aspects. In such cases grouping (estimation of monophyletic groups) will proceed solely by study of patterns of synapomorphy (i.e. shared, derived characters), and a practical ranking concept must be used until something becomes known about biology. This preliminary and pragmatic ranking concept will usually be the size of morphological gaps (i.e. number of synapomorphies along any particular internode of a cladogram) in most cases, a concept in accord with current taxonomic practice.

The phylogenetic species concept (PSC) of Mishler and Donoghue can be summarized 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 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.

Relating the PSC back to the earlier discussion of individuality, it is clear that species so defined (as with monophyletic taxa at all levels) will at least meet the restricted spatio-temporal criterion of individuality. They may or may not be integrated or cohesive. However, these criteria may often prove useful in ranking decisions. Since the strength of integrative or cohesive bonds tends to gradually weaken as more and more inclusive groups of organisms are taken (see e.g. the discussion in Mayr 1987), it may be possible in many cases to objectively fix the species level as the most inclusive monophyletic group that is integrated or cohesive with respect to 'important' processes. Again, 'important' has a context-dependent meaning, and will often not refer to reproductive criteria. It may often be difficult to apply this standard, especially if macro-evolutionary processes occur (even rarely) involving groups at high taxonomic levels (Gould 1980, Jablonski 1986). If so, integrated and/or cohesive groups may occur at *much* more inclusive levels than anyone would wish to name as basal taxonomic units.

The problem of (at least partial) non-comparability of species taxa in different groups of organisms is a real one (Sober 1984, Hull 1987, Ghiselin 1987). However, as pointed out by Mishler and Donoghue (1982), this has always been the case, despite the fact that many users of species taxa—ecologists, philosophers, palaeobiologists, biogeographers, for example—remain blissfully unaware. This difficult situation has not come about because (as suggested by Ghiselin (1987)) systematists working with organisms other than birds are incompetent, but rather reflects a fact of nature. The pluralistic ranking concept of the PSC was proposed to allow different biological situations to be explicitly treated. Persons interested in studying some biological process simply cannot avoid the responsibility of learning enough about the systematics of the organisms they are studying to ensure that the entities being compared are truly comparable with respect to that process.

To take one example that has been widely recognized (Mayr 1987), asexual organisms present insurmountable difficulties for the biological species concept. One proposed solution has been to deny that such organisms form species (Bernstein *et al.* 1985, Eldredge 1985, Hull 1987, Ghiselin 1987). This *reductio ad absurdum* of the biological species concept demon-

strates how a monistic ranking (and grouping) concept based on interbreeding criteria can obscure actual patterns of diversification. One of us happens to work on a genus of mosses (*Tortula*, see Mishler 1985 for references), in which frequently sexual, rarely sexual, and entirely asexual lineages occur. The interesting thing is that the asexual lineages form species that seem comparable in all important ways with species recognized in the mostly asexual lineages and even in the sexual lineages.³ It just happens in this case that potential interbreeding or lack thereof seems of little or no importance in the origination and maintenance of diversity. The application of the PSC here is able to reflect an underlying unity that the biological species concept could not.

Indeed, there seems to be a fundamental confusion at the heart of the biological species concept and its insistence that only sexual organisms can form species. *Potential* interbreeding and the lack thereof (i.e. breeding barriers) can be observed in nature, and so can be used as a ranking criterion for species. But why should it be so used, or rather, why should it be the only ranking criterion used? We suspect that part of the rationale stems from a confusion over the roles of potential interbreeding and actual interbreeding.

Actual interbreeding is a process. It results in lineages (but not always lineages important enough to be named species—for example, short-lived hybrid populations). The process of (actually) interbreeding also inevitably leads to a certain amount of integration. In sexual species it undoubtedly is one of the important processes holding the species together. But potential interbreeding is not a process, and therefore has no effect on the integration or cohesion of species. The dispersed parts of a sexual species are not bound together by this non-process; they may be bound together by sharing common environments or common developmental programmes, but they cannot be bound together by 'potential interbreeding'.

In general, the potential to interbreed is based on organisms sharing common environments and common developmental programmes. The processes that result in groups of organisms sharing such features and in discontinuities between such groups are multifarious, and are not restricted to sexual organisms. Organisms share common developmental programmes because they share a common ancestor. Reproduction is a relevant process here, but not necessarily sexual reproduction.

³ A similar result has been arrived at by Holman (personal communication), based on comparisons between bdelloid rotifers (which are exclusively parthenogenic) and monogonont rotifers (which occasionally reproduce sexually). Using numbers of synonymous species names as an index of taxonomic distinctness of species, he has shown that bdelloid species are apparently more consistently recognized by taxonomists than are monogonont species.

It is our argument that the PSC is superior to the biological species concept (or to the evolutionary species concept of Simpson (1961) and Wiley (1978), which is similar in these ways to the biological species concept) in two fundamental ways. First, monophyly as a grouping criterion is superior to ability to interbreed, because it will lead to a consistently genealogical classification. Second, the pluralistic ranking concept of the PSC is superior to the monistic insistence on breeding barriers of the biological species concept because it can more adequately reflect evolutionary causes of importance in different groups.

Other cladistic species concepts, such as the 'phylogenetic species concept' of Cracraft (1983), which is very similar to the species concept of Nelson and Platnick (1981), are also inferior to the PSC of Mishler and Donoghue, but for somewhat different reasons. The grouping concept used by the former authors (i.e. a cluster of organisms defined by a unique combination of primitive and derived characters) does not rule out the possibility of paraphyletic species, unlike the PSC (see next section). Furthermore, the concepts of Cracraft and Nelson and Platnick (in addition to the concept of Rosen (1979), that *does* use presence of synapomorphies as a grouping criterion) are incomplete, in that they lack a ranking criterion. It is not sufficient to say that a species is the smallest diagnosable cluster (Cracraft 1983) or even monophyletic group, because such groups occur at all levels, even *within* organisms (e.g. cell lineages). Some judgement of the significance of discontinuities is needed.

Monophyly

One final area in need of clarification is the concept of monophyly. Traditionally, the cladistic definition of monophyly (which we favour) has not been applied to the species level. Henning (1966) did not do so because he was committed to a biological species concept, and thought that there was a clean break at the species level, with reticulating genealogical relationships predominating below and diverging genealogical relationships predominating above. Later cladists (e.g. Wiley 1981) have followed Hennig and defined a monophyletic taxon as one that originated in a single species and that contains all descendants of that species. Species are taken to be monophyletic a priori; therefore it is argued that they need not possess synapomorphies or really be monophyletic in the sense of higher taxa (e.g. Wiley 1981). One major reason for this is the supposed problem on 'ancestral' species.

It is our view that, properly clarified, there are no insurmountable problems with applying the concept of monophyly explicitly to species (as the

basal systematic taxon). Furthermore, this application *must* be carried out in order to have a consistently genealogical classification.

Monophyly should be redefined in such a way as to apply to species:

A monophyletic taxon is a group that contains all and only descendants of a common ancestor, originating in a single event.

'Ancestor' here refers, not to an ancestral species, but to a single individual. By 'individual' here, we do not necessarily mean a single organism, but rather an entity (less inclusive than the species level) with spatio-temporal localization and with either cohesion or integration or both (as defined above). In particular cases this ancestral individual could be a single organism, a kin group, or a local population. We would argue that it would never be a whole species, because we share the widespread view that new species come about only via splitting, not by any amount of anagenetic change.

The originating 'event' of a monophyletic group referred to in the definition above could be due to the spatio-temporally restricted action of a number of different causes. These could include, in different cases, the origin of an evolutionary novelty which causes a new monophyletic group to be subject to a different selective regime than the rest of the 'parent' species or which causes a disruption of the normal developmental canalization of the 'parent' species. These could also include acquisition of an isolating mechanism or even the origin of a new species by hybridization between parts of two 'parent' species. This diversity of causes for evolutionary divergence reinforces the need for a pluralistic ranking concept.

Some examples of the application of this concept should clarify the definition. It is thought at the present time that a common mode of speciation is via peripheral isolation. In such a case, the peripherally isolated part of the species, if spatio-temporally localized (say, on the same island at the same time) and either cohesive, integrated, or both (say, by interbreeding and sharing a common niche), would qualify as a monophyletic group under our definition. This would be true even if several rather unrelated members of the original species were the founders of the peripheral population, as long as the above conditions obtain. On the other hand, if two similar but non-spatio-temporally connected peripheral populations (say, on two different islands) have been established by members (even closely related ones) of the original species, these two populations would have to be considered as two separate monophyletic groups. They are two separate monophyletic groups, because they originated in two different events. Hybrid speciation provides similar examples. If two original

Why not treat these closely related members as the original monos. group? Where the event is whatever prompted the (divergent) per. isol?

species produce a hybrid population in one place (say, a single valley) at one time (say, in a single breeding season), and if this hybrid population behaves as an integrated and/or cohesive entity, then it is a perfectly good monophyletic group under our definition. However, if similar hybrids are produced elsewhere in the ranges of the two original species, or if hybrids are produced in the *same* locality but discontinuously in time (i.e. if the first hybrid population goes extinct *before* the new hybrids are produced), then the separate hybrid populations would have to be considered as separate monophyletic groups, and could not be taken together and named as a new species. Note that this conclusion is directly opposite that of Kitcher (1984b: 314–15). The implications of our concept of monophyly for the *original* species in the above examples will be discussed below.

This concept of monophyly is, of course, only a grouping criterion. It does not imply that any particular peripheral isolate or hybrid population must be recognized as a species. It only specifies the genealogical conditions under which such groups can be recognized if the ranking criterion applied in a particular case supports recognition at the species level. The grouping and ranking criteria can thus be seen to interact in producing a species classification. Note that a corollary of the PSC is that not all organisms will belong to a formal Linnaean species, since some monophyletic groups (e.g. hybrid populations that arise, but then quickly go extinct) will not be judged to be 'important' monophyletic groups. The hybrid organisms in such a case would not formally belong to either original species.

The definition of monophyly given above solves the problem perceived by Hennig (1966), Wiley (1981), and Cracraft (1983) with 'ancestral species'. No such things exist. Only parts of an original species give rise to new ones, as in the above examples. If a currently recognized species is found to be paraphyletic, because parts of it can be demonstrated to be more closely related to another species (Fig. 14.1; see also discussions and diagrams of such a situation in Bremer and Wanntorp 1979, Avise 1986), then the paraphyletic species should be broken up into smaller monophyletic species.

Note that if species 1 (Fig. 14.1) is actually integrated by gene flow, then over time its cladistic structure should approach that of species 1 in Figure 14.2. Moreover, over an even longer time in such a truly integrated species, patterns of character distribution should even out such that no autapomorphies remain to distinguish lineages within the species, and species 1 would be represented in a cladogram by a single line (albeit still without any synapomorphies to distinguish it as a species). In systematic studies, a situation is frequently encountered (Fig. 14.2) in which a number of unre-

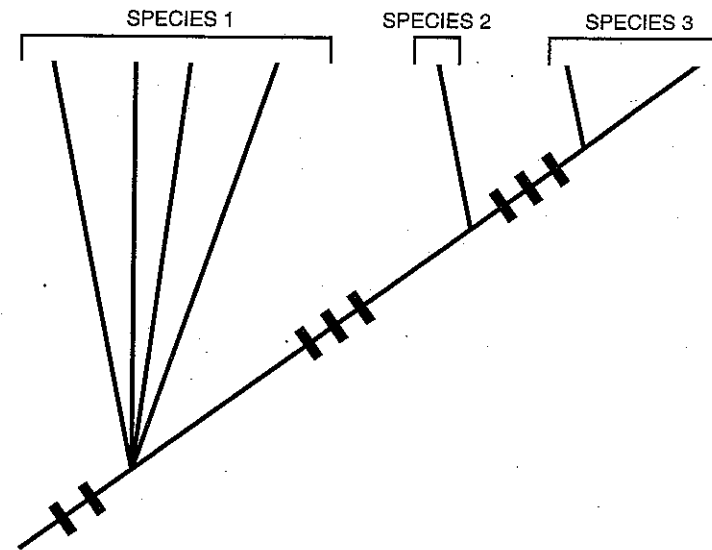


Fig. 14.2. A hypothetical cladogram showing three named species. Synapomorphies are shown as cross-bars; autapomorphies are not shown. Species 1 is paraphyletic.

solved lineages exist, one or more of which are deemed worthy of recognition as separate species, and the rest of which have traditionally been considered a species taken together. This type of situation has been confused with paraphyly. However, it is actually a case of a taxon (e.g. species 1 in Fig. 14.2) with an uncertain status between paraphyly and monophyly. With further study, synapomorphic characters may be found uniting some part of species 1 with the lineage of species 2 and 3 (as in Fig. 14.1). If that becomes the case, species 1 truly is paraphyletic and must be broken up. On the other hand, further study may demonstrate synapomorphies uniting all of the lineages in species 1, thus making it an unproblematic phylogenetic species.

It has been cogently argued by Donoghue (1985) that a group such as species 1 in Figure 14.2 could acceptably be named a species in a tentative and pragmatic way, pending further study designed to resolve the relationships, as long as a special convention was followed to indicate the uncertain status of the species (Donoghue suggests marking the binomial name of all such species with an asterisk). This solution is practical, because it avoids unnecessary naming of highly localized species (if, for example, all

recognizable lineages in species 1, Fig. 14.2, were formally named). It is also probably unavoidable, since if speciation by peripheral isolation occurs frequently, such situations may often be in principle unresolvable, as discussed above. Donoghue (1985) suggested calling this type of species a 'metaspecies', to clearly distinguish it from a known monophyletic species. Following the prefix he suggested, we suggest the need for a new term, 'metaphyly', to refer to the status of groups that are not known to be either paraphyletic or monophyletic. Although beyond the scope of the present essay, this term would clarify similar situations with respect to higher taxa, and may thus prove more widely useful.

CONCLUSION

The 'species problem' as discussed here involves a search for a definition of the basal systematic unit that will be at once practical, provide optimal general-purpose classifications, and reflect the best current knowledge about evolutionary processes. We have claimed that the PSC will fulfil these criteria. However, we certainly have not claimed that *all* important biological entities can be recognized using the PSC.

As pointed out clearly by Holsinger (1984), a multitude of interesting biological entities, often non-overlapping, are behaving as (at least partial) individuals with respect to a multitude of interesting processes in any particular group of organisms. While we do need to settle on criteria for recognizing formal taxa for our Linnaean taxonomic system (including species), we are of course in no way prohibited from informally naming and studying other entities of interest that do not fit the formal taxonomic system—that is, as long as different types of entities are explicitly distinguished from each other.⁴

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- ⁴ We dedicate this essay to Ernst Mayr, even though he probably disagrees with much of its contents. At different times and in different ways, we both were profoundly affected by our interactions with him during our graduate careers at Harvard. We thank him for his advice, insights, and patience. We also thank David Hull and Marjorie Grene for comments that helped to clarify certain aspects of the paper. Eric Holman kindly allowed us to cite his unpublished data on rotifers.
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PHYLOGENETIC SYSTEMATICS AND THE SPECIES PROBLEM

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[T]he task of 'ordering' (and what means the same thing, of systematics) lies in considering the unit as a member of an ordered whole. It is a fact . . . that no unit exists as a member of only one whole.

Therefore it is possible to arrange animated natural things in numerous different systems, depending on which of these different relationships has been investigated. The differences among all these systems are determined by the particular relationships of which they are a concrete expression. All these different systems are, fundamentally, equally justified so long as they are a proper expression of the membership position that an object of nature possesses within the framework of the totality, for the dimension that was chosen as the basis for the particular system.

The different systems . . . are not unrelated to one another. The relations between them . . . can themselves be made the subject of scientific systematic investigation. On the other hand, it is not basically a scientific task to combine several systems so created, because one and the same object cannot be presented and understood at the same time in its position as a member of different totalities.

Hennig, *Phylogenetic Systematics*

INTRODUCTION

Darwin established the fact of evolution—the process of descent with modification—and its product, phylogeny. Although he predicted that taxonomies would become; 'as far as they can be so made, genealogies' (Darwin 1859: 486), the widespread acceptance of evolution did not lead to a major re-evaluation of the goals, principles, and methods of taxonomy. Instead, existing taxonomies simply were reinterpreted in evolutionary terms. That is, the reality of previously recognized taxa was taken for

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granted, and evolutionary concepts and mechanisms were formulated to account for their existence (Stevens 1984, de Queiroz 1988).

During the 'modern synthesis' several authors, Mayr and Simpson in particular, explored the link between taxonomy and evolutionary theory. Their widely accepted conclusion was that species are fundamentally different from taxa at both higher and lower categorical levels. Species, unlike other taxa, are not only an outcome of evolution; they actually function in a direct way in the evolutionary process: as gene pools in the case of Mayr, and as lineages extending through time in the case of Simpson. Species were seen to exist as wholes—that is, to be real things—whereas other taxa were viewed as subjective and arbitrary (Mayr 1963: 600–1, 1969b: 91–2; Simpson 1961: 188–91).

From the perspective of developing evolutionary systematics, perhaps the most significant aspect of the views of Mayr and Simpson was that existing species taxa were not taken as given. Although these concepts may have been formulated initially as theories to explain the existence of groups having common morphologies or ecologies, they quickly became prescriptions about how the species category should be defined, and as such they necessitated a re-evaluation of the status of existing taxa (Donoghue 1985). Because the species category was defined in such a way that its members would be participants in the evolutionary process, the basal taxonomic unit became a fundamental evolutionary unit (e.g. Simpson 1961; Hull 1965, 1976, Mayr 1969a, 1982).

This outlook contrasts sharply with an alternative view in which species concepts are treated as theories meant to explain the existence of already recognized taxa (e.g. Mishler and Donoghue 1982: 494), a perspective that has hindered the development of systematics. By accepting the reality of previously recognized taxa, concepts associated with important biological processes are relegated to the role of after-the-fact explanations for the existence of these taxa, instead of functioning as central tenets from which real entities and the methods for their discovery are deduced (cf. de Queiroz 1988).

Hennig (1966) did for the development of evolutionary systematics above the 'species level' what Mayr and Simpson had done with regard to 'species'. That is, he changed the role of evolution as it relates to 'higher' taxa, from an after-the-fact interpretation of the order already manifest in taxonomy to a central tenet from which he deduced what entities exist as its natural outcome (de Queiroz 1985). According to Hennig, the products of evolution above the 'species level' are groups composed of ancestral species and all of their descendants—complete systems of common ancestry—clades—monophyletic groups. Inasmuch as monophyletic groups are

a natural outcome of the process of evolutionary descent, they are real and exist as wholes outside of the minds of taxonomists.

Hennig's concept of monophyly was seen by some later authors to have implications not only for taxa at 'higher' categorical levels but also for those at the 'species' level. In particular, Rosen (1978, 1979) and Bremer and Wanntorp (1979) argued that reproductive compatibility might be lost in a mosaic pattern among the populations descended from a common ancestor in such a way that the ability to interbreed, as a retained ancestral trait, would be uninformative about recency of common ancestry. Consequently, if organisms or populations were assigned to species taxa on the basis of this ability, then some species would be paraphyletic. This conclusion has led some authors to argue against species concepts based on interbreeding and to develop species concepts based on monophyly (Mishler and Donoghue 1982; Cracraft 1983, 1987; Ackery and Vane-Wright 1984; Donoghue 1985; Mishler and Brandon 1987; McKittrick and Zink 1988). They argue that there is not (or at least there should not be) a basic difference between species and other taxa; some monophyletic groups are simply more inclusive than others.

In short, a tension has developed around species concepts that involves ideas central to evolutionary biology in general and phylogenetic systematics in particular (cf. Løvtrup 1987: 172–3). Here we explore some manifestations of this tension and their significance for phylogenetic systematics, especially as they bear on a choice among alternative species concepts. Nevertheless, we advocate neither a new species concept nor any existing one. Instead, we develop a way of looking at the species problem that builds upon the conceptualization of systematics expressed in the epigraph. Central to this view is a consideration of different kinds of entities that exist in nature and their relationships to one another.

MONOPHYLY

Tension between the significance of interbreeding and common descent is evident in discussions of the kinds of entities to which the concept of monophyly properly applies. Some arguments simply define the conflict out of existence. Platnick (1977), Willmann (1983) and Ax (1987), for example, considered it inappropriate to enquire whether species are monophyletic, paraphyletic, or polyphyletic, claiming that these terms apply only to groups of species. This position unnecessarily restricts the concept of monophyly, and overlooks the fact that species themselves are 'groups' (groups of organisms). Regardless of precedents set by previous

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authors, there is no biological reason not to view monophyly, paraphyly, and polyphyly as general concepts wherein the units of common ancestry are unspecified. Thus, these terms can be applied not only to groups of species, but also to groups of any entities that reproduce and thus form ancestor-descendant lineages. Under this view it is legitimate to ask whether a particular organism is or is not a monophyletic group of cells, whether a particular population is a monophyletic group of organisms, or whether a particular species taxon is a monophyletic group of populations—as legitimate as it is to enquire whether a particular 'higher' taxon is or is not a monophyletic group of species.

Wiley (1977, 1979) attempted to resolve the conflict between interbreeding and monophyly in another way. He claimed that species 'are a priori monophyletic by their very nature' (Wiley 1979: 214). In effect, his proposition is that because species have 'a real existence in nature', therefore they are monophyletic. But this implies that there is only one kind of existence. If 'species' and monophyletic groups exist in different ways, then 'species' can exist without being monophyletic.

Other authors allow that it is legitimate to enquire whether species are monophyletic, but, unlike Wiley, they conclude that some species—namely, ancestral ones—are paraphyletic. Brothers (1985) coupled this idea with the notion that asexual organisms form evolutionary species (*sensu* Simpson 1961, Wiley 1978), and concluded that paraphyletic higher taxa are meaningful evolutionary groups. This follows from his assertion that the relationship between asexual species and their component organisms is analogous to that between higher taxa (including paraphyletic ones) and their component species.

Brothers's argument hinges on the false premiss that paraphyletic sexual and asexual 'species' exist in the same way. Paraphyletic asexual 'species', however, are not unified by interbreeding, as are sexual 'species'; instead, they are defined solely by phenetic similarities and gaps. (Brothers 1985: 36). In fact, the only connection between sexual and asexual 'species' in Brothers's argument is that both are supposedly accommodated under the evolutionary species concept. The evolutionary species concept (Simpson 1961), however, refers to 'a single lineage of ancestral descendant populations' (Wiley 1978: 18); and to equate the kinds of lineages formed by sexual and asexual organisms under the term 'evolutionary species' is to confuse two different uses of 'population'. Only the unjustified acceptance of phenetically delimited, paraphyletic collections of asexual organisms as 'real evolutionary species' supports Brothers's contention that paraphyletic higher taxa are acceptable evolutionary groups (see Donoghue 1987 for additional discussion).

The arguments of Wiley and of Brothers are similar in one important respect—both tacitly assume that different kinds of entities exist in the same way: monophyletic groups and 'species' in the case of Wiley, sexual and asexual 'species' in the case of Brothers. Others—for example, Eldredge and Cracraft (1980)—have argued that there is a fundamental difference between sexual species and monophyletic higher taxa. They allow that some species—namely, ancestors—are not monophyletic, but they consider this to be acceptable because species exist in a different way: namely, as individuals. For Eldredge and Cracraft (1980: 90), monophyletic groups exist, but are not necessarily individuals, whereas species exist because they are individuals.

INDIVIDUALITY

The concept of individuality has figured prominently in many recent discussions of species concepts, including several of those discussed above. That organisms are not the only kind of biological 'individuals' follows from accepting that living matter is organized into wholes that are themselves parts of more inclusive wholes. Although Ghiselin (1966, 1974, 1981, 1985) and Hull (1976, 1977, 1978) deserve credit for popularizing and developing the idea that species are appropriately viewed as individuals in the philosophical sense, very similar ideas were set forth independently by Hennig (1966) and Griffiths (1974), whose discussions of the individuality of biological taxa stem from the writings of even earlier authors (i.e. Woodger 1952, Gregg 1954).

The concept of individuality is commonly illustrated by contrasting individuals with classes and describing characteristics of each (Ghiselin 1974; Hull 1976, 1977, 1980, 1981). Classes have members; individuals have parts. Classes are spatio-temporally unrestricted; individuals are localized in space and time. The names of classes are usually defined 'intensionally' (i.e. by listing the attributes that are necessary and sufficient for membership); the names of individuals are proper names, and can only be defined 'ostensively' (i.e. by showing the object to which the name is given). The members of a class are similar, in that they share at least the attributes that define the class name; the parts of an individual need not be, and frequently are not, similar. Beyond this general characterization, however, there are more and less restricted concepts of individuality. Thus, according to Hull (1978) and Wiley (1981), individuals must not only be spatio-temporally localized but also must be continuous and cohesive. These last

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two terms require special attention, as they bear directly on the existence of different kinds of entities that have organisms as parts.

Continuity

There are at least two different forms of continuity: current and historical. Wiley (1981) made current continuity an explicit component of his concept of individuality. He did not, however, distinguish between current continuity and cohesion, for he considered both to result from the same process (at least in sexual species): namely, reproductive ties among organisms. In contrast, Ghiselin (1974) explicitly rejected current continuity as a necessary component of individuality, arguing that the United States of America is an individual nation, despite the physical discontinuity between Alaska and the remainder of the continental United States. The truth of this example notwithstanding, at least some kinds of individuals (e.g. multi-cellular organisms) result from direct physical connections among their parts, and in these cases continuity is inescapable. It appears, then, that whether current continuity is a necessary component of individuality depends upon the nature of the phenomenon conferring individuality.

Historical continuity has been identified as the unbroken chain of descent from a common ancestor (e.g. Ghiselin 1980, Wiley 1981). While this applies to some kinds of individuals (e.g. monophyletic groups), it does not seem to be a necessary component of individuality. An organism, for example, does not cease to be an individual when it receives an organ transplant; nor does a population of interbreeding organisms cease to be an individual when it receives immigrants. As in the case of current continuity, it seems that whether historical continuity is necessary for individuality depends on the nature of the phenomenon conferring individuality.

Cohesion

The presence or absence of cohesion has been considered an important difference between 'species' and monophyletic higher taxa (e.g. Hennig 1966, Wiley 1981, Ghiselin 1985). Unfortunately, ambiguities still plague this critical issue, some of which are clarified by considering the meaning of 'cohesion' and the biological phenomena that might confer it.

'Cohesion' is commonly used to mean 'sticking together' (e.g. Webster's *New International Dictionary*, 2nd edn.); thus, cohesion is a property that might confer individuality by uniting parts to form a whole. The cells that make up a multi-cellular organism are physically stuck together, but at the

'species level' cohesion is less obvious. According to Wiley (1981), cohesion among the parts of a species composed of sexually reproducing organisms is maintained by reproductive ties (see also Brooks and Wiley 1986: 48-9). In contrast with the biological species concept (e.g. Mayr 1942), however, only actual interbreeding matters in this context (cf. Hull 1965). If cohesion is conferred by interbreeding, then the potential to interbreed allows only the potential to cohere. That interbreeding is widely considered to be the process conferring 'species level' cohesion is evident from the commonly stated view that asexual organisms do not form 'species' (e.g. Bernstein *et al.* 1985: 328). As Hull (1980) put it, 'strictly asexual organisms form no higher-level entities; organism lineages are the highest level lineages produced'.

Other than sexual reproduction, no biological process has been identified that might confer cohesion at the 'species level'. Although interactions other than interbreeding seem to confer cohesion on groups of organisms that make up colonies or symbiotic partnerships, these entities are never called 'species'. Several other phenomena have been suggested as 'species level' agents of cohesion, but such proposals confuse cohesion with constraint or inertia. Wiley (1981), for example, considered that stasis maintains cohesion among the parts of 'species' composed of either sexual or asexual organisms (see also Mishler 1985, Mishler and Brandon 1987). Stasis may result from either extrinsic or intrinsic constraints, such as stabilizing selection or the resilience of developmental systems. Although such phenomena may cause organisms to remain similar, this is not the same as 'sticking together'. When discussing biological individuals having organisms as their parts, cohesion must refer to interactions among those organisms. Shared genetic or developmental programmes, or common mate recognition systems (Paterson 1978, 1985), or any other properties that organisms might have in common, no matter how biologically significant, are not interactions among those organisms.¹ Although some of these properties may allow cohesive interactions to occur among organisms, they do not, by themselves, constitute cohesion.

Although cohesion has often been associated with individuality, it is not required by every version of the concept. Thus, according to Ghiselin (1974), an individual is simply 'a particular thing'. This is compatible with the view taken by Hennig (1966), Patterson (1978), Ghiselin (1969, 1980,

¹ Vrba (1985) suggested a 'fundamental compatibility between the "individual" and "recognition concepts" of species', at least in part because both 'draw on the reproductive activities among organisms'. Nevertheless, under Paterson's recognition concept, species are classes defined by similarities and differences in characters that make fertilization possible; actual reproduction, or even actual mating, are not required (see Donoghue 1987).

This seems
an artificial
kind of
'individual'

Now that's
better than
before!

Probably
don't trust
the

Of course
if you
have those
in common
they may
also be
interacting
in some
way.

Why
is it
not
the
same
as
sticking
together?

1985), Griffiths (1974), and Hull (1976) that monophyletic higher taxa are individuals, despite the fact that they do not exhibit cohesion among their parts, each being made up of independently evolving lineages (Wiley 1980, 1981). Wiley (1980, 1981) stressed this basic distinction by coining the term 'historical group' for monophyletic higher taxa (which are historically continuous), and restricting 'individual' to cohesive entities such as 'species'. Ghiselin (1985) accepted this distinction, but preferred a classification in which 'individual' includes both non-cohesive historical groups and cohesive units (which he called 'integrated wholes').

We conclude that several different kinds of entities have been called individuals. Consequently, the individuality 'revolution' (Ghiselin 1987) may be partially responsible for obscuring significant distinctions between them. The view has developed that individuals are things with a real existence in nature; for this reason, if something is said to be an individual, it seems to gain significance. Simply asserting that something is an individual, however, does little to clarify the nature of its existence. Inasmuch as one kind of individual may be significant for one theory but not for another, it is necessary to go beyond individuality and answer the question 'individual what?'. In the next section our aim is to focus attention away from individuality *per se*, and instead to explore those phenomena that confer existence on certain entities that have been identified as individuals.

SYSTEMS

The nature of existence of wholes is clarified by adopting the perspective of systematics formulated by Griffiths (1974) and has been discussed recently by de Queiroz (1988). These authors distinguished between classification, the ordering of entities into classes, and systematization, the ordering of entities into systems. Classification and systematization differ fundamentally, in that classes are groups whose members belong to those groups because they share some attribute(s), whereas systems are wholes that derive their existence from some natural process through which their parts are related (de Queiroz 1988). Ghiselin (1974) pointed out that the term 'individual' can designate systems at various levels of integration, which suggests that the different kinds of entities previously identified as individuals might be viewed as kinds of wholes deriving their existence from different underlying natural processes. This perspective facilitates discrimination among different kinds of individuals by focusing directly upon the natural processes responsible for their existence.

		interbreeding	
		+	-
Common descent	+	I +	III -
	+	+	+
	-	II +	IV -
	-	-	-

FIG. 15.1. Possible relations between cohesive wholes resulting from the process of interbreeding and monophyletic groups resulting from the process of common descent. The presence of each process is symbolized by +, and absence by -.

We have identified two processes through which organisms are related: interbreeding and common descent. Exploration of the systems resulting from these different processes and the relations between them is facilitated by constructing a table with interbreeding (resulting in one kind of cohesive whole) along one axis and common descent (resulting in monophyletic groups) along the other (Fig. 15.1). Entities in the upper left-hand box of this table (labelled I) are both cohesive and monophyletic; entities in the lower left-hand box (II) are cohesive but not monophyletic; and so forth. The word 'individual' has been applied by one author or another to entities in each of the first three boxes. Any entities in box IV are either systems deriving their existence from some natural process other than interbreeding or common descent, or they are recognized simply because their members share certain traits, and therefore are classes. In the latter case, regardless of the importance of the traits upon which such groups are based, they do not qualify as systems. Unless their parts are related through some natural process, such classes do not exist as wholes. Included

Says who? this seems
utterly arbitrary.

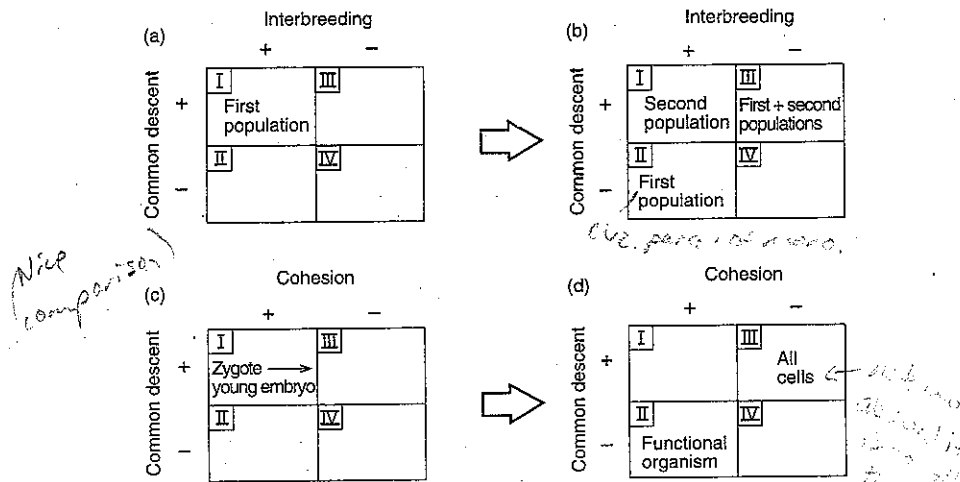


FIG. 15.2. Entities followed through time as categorized in Fig. 15.1. (a) A young population descended from a single gravid female. (b) System (a) after the establishment of a new population. (c) A young embryo descended from a single zygote. (d) System (c) after some cells have died and been sloughed off.

here are paraphyletic and polyphyletic higher taxa, which must be viewed either as aggregations or collections of less inclusive wholes, or as parts (incomplete systems) of more inclusive wholes.

Because two different processes are being considered, a group of entities that forms a system resulting from one of the processes may or may not also form a system resulting from the other (cf. Holsinger 1984). This point is easily visualized by using the table in Figure 15.1 to follow groups of entities through time (Fig. 15.2). Suppose, for example, that we begin with a gravid female of some kind of sexually reproducing organism. She and her offspring establish a population within which there is steady interbreeding between component organisms. For the sake of simplicity, let us further suppose that no deaths occur. For a time this population resides in box I—it is both a monophyletic group of organisms and a group that is cohesive as a result of interbreeding (Fig. 15.2a). Now imagine that at some later time another gravid female leaves this population and successfully establishes a new population that is geographically separated from the first, so that the two populations are reproductively isolated by distance. At this point (Fig. 15.2b) the first population shifts into box II—it is no longer a monophyletic group of organisms; however, it remains a cohesive

entity. The first and second populations, taken as a unit, now occupy box III, because together they constitute a monophyletic but non-cohesive group. Finally, the newly established population begins its existence in box I.

The point of this exercise is that there may be switches between boxes or states of existence, and one is free to focus attention on entities belonging to any of the classes in the table of possibilities. Thus, we might choose to focus on interbreeding systems, on those resulting from common descent, or on both. There is no right or wrong in this; one is not better than another, or generally more significant. The entities in the upper row of boxes and those in the left-hand column all exist, but they exist in different ways: that is, they exist as the outcome of different processes. Furthermore, in box I, wholes deriving their existence from one of the processes correspond precisely with (have the same parts as) wholes deriving their existence from the other process.

It is worth noting that the framework developed above is a general one, which is to say that other forms of cohesion and common descent may occur at different levels of organization. For example, instead of following groups of organisms, one might focus on groups of cells (Fig. 15.2c, d). Following the first few mitotic divisions, the group of cells making up an embryo is integrated into a cohesive whole by physical and chemical interactions; these also form a monophyletic group of cells descended from the zygote. This group of cells therefore exists in box I (Fig. 15.2c). At a later time during development (Fig. 15.2d), some cells die and are sloughed off the embryo (or perhaps the embryo is split into two cohesive wholes, as in the case of identical twins). After this point we might choose to follow the fate of the functioning organism, which remains a cohesive whole, but is no longer a monophyletic group of cells. Alternatively, we might focus on the set of all cells descended from the zygote, even though these are no longer all integrated in one functioning body.² Traditionally, attention has been focused on the cohesive organism, but there may be some purposes for which it is necessary to keep track of the monophyletic group of cells—for example, in studying the frequency of somatic mutations.

The foregoing analysis emphasizes that the tension surrounding species concepts results from there being different kinds of real biological entities.

² A monophyletic group consists of an ancestor and all of its descendants. Thus, the dead and sloughed-off cells are part of the monophyletic group of cells descended from the zygote, although they are no longer part of the functioning organism. Similarly, monophyletic groups of organisms include dead organisms, even though these are no longer parts of interbreeding populations, and monophyletic 'higher taxa' include extinct and unknown subgroups.

why would we want to do this? got. But would we ever call this an indiv.

Some of these entities exist as an outcome of a process conferring cohesion, while others exist as an outcome of descent from a common ancestor. And sometimes an entity that exists as the consequence of one of these processes happens to correspond exactly with one that exists as a consequence of the other. Before we can explore how these conclusions bear on the species problem, it is first necessary to examine some assumptions and limits of phylogenetic systematics.

PHYLOGENETIC SYSTEMATICS

Adopting the view that systematics is the discovery of entities that derive their existence from some underlying natural process implies that phylogenetic systematics is that kind of systematics in which the process of interest is evolutionary descent (de Queiroz 1988). The methods of phylogenetic systematics are based on the premiss that there exists an evolutionary tree and, therefore, a nested hierarchical pattern of relationships. This implies that it is inappropriate to apply cladistic methods to entities that are expected *not* to be related in a nested hierarchical pattern: that is, entities related in some other pattern, such as a reticulum of intersecting sets. In other words, there are identifiable limits to the sensible application of phylogenetic methods, boundaries beyond which it is fruitless to proceed.

The exact nature of these limits depends on the properties of the entities under investigation. In the case of sexually reproducing organisms, a limit is set by the level at which continually branching (diverging) relations give way to predominantly reticulate relations resulting from interbreeding. It is inappropriate to enquire about phylogenetic relationships among actually interbreeding organisms, because here the pattern of relationships is not a nested hierarchy (cf. Hennig 1966: 18–19). Phylogenetic methods break down in this case, because an assumption underlying the principle that shared derived characters provide evidence of phylogenetic relationship (i.e. of monophyly) is violated. Thus, in the case of sexual dimorphism, grouping by shared derived characters may lead to the false conclusion that the males (for example) within a population of interbreeding organisms form a monophyletic group. The problem in this case is that sex-linked traits of the males are being interpreted as synapomorphies at the wrong level, a fact that would become evident upon examining the distribution of these traits among parents and their offspring.

Populations themselves, by contrast with their component organisms, may show a branching pattern of relationship to one another. Indeed,

using populations as terminal taxa will potentially yield the finest possible resolution of phylogenetic relationships among sexually reproducing organisms. Populations, therefore, have a special role as 'basal units' in the phylogenetic systematics of organisms.³ This role is entirely independent of whether these units are monophyletic, but instead is an outcome of the process of interbreeding.

In the case of organisms that reproduce only asexually, the limits of phylogenetic analysis are different. Here, in contrast to the reticulate relationships that result from sexual reproduction, the pattern of common ancestry among asexual organisms forms a nested hierarchy. Whether asexual organisms are monophyletic or paraphyletic groups of cells, relationships among them are amenable to phylogenetic analysis, because these organisms are cohesive wholes that form diverging lineages.⁴

Hennig (1966: 29–32) delimited the scope of phylogenetic systematics in distinguishing parts of 'the total structure of hologenetic relationships'. His figure 6 (our Fig. 15.3) shows semaphoronts linked into semaphoront groups (individual organisms) through ontogenetic relationships, and organisms linked through 'tokogenetic relationships' into species. Phylogenetic relationships were limited by Hennig to those above the level of interbreeding groups—to relationships among 'species'. Most of Hennig's discussion assumed a sexual mode of reproduction. Regarding cases of asexual reproduction, he noted that the differences between ontogenetic, tokogenetic, and phylogenetic relationships are blurred. Nevertheless, he concluded that even in asexual groups 'it is possible to delimit in the fabric of hologenetic relationships an area that lies between the more or less

³ Throughout this essay we mean by 'population' units within which interbreeding between organisms of different sub-units is sufficient such that the relationships among these sub-units are reticulate, while relationships among the units themselves are predominantly diverging. Consequently, the units that qualify as populations depend upon the time-scale under consideration. Over short time periods, there may be a diverging pattern of relationships among demes, and this is potentially recoverable through cladistic analysis. This pattern of relationships, however, may be obliterated over longer periods of time if there is sufficient gene flow among demes so that they function together as a single population.

⁴ The cohesion responsible for the existence of individual organisms, whether sexual or asexual, does not involve reticulate patterns of descent among their component parts. Therefore, phylogenetic analysis can be extended down to the level of cells, or even to parts of cells (e.g. organelles, chromosomes, 'genes'). This is done, for example, in analysing the propagation of somatic mutations within and between the meristems of plants (Whitham and Slobodchikoff 1981, Klekowski *et al.* 1986; see Buss 1983, 1987, for examples in animals). However, parts that reproduce can begin diverging prior to the divergence of more inclusive wholes. This occurrence, in conjunction with differential sorting of variant parts within higher-level lineages, can result in non-correspondence between phylogenetic relationships among entities at different levels (Kawata 1987). For example, mitochondria, which form lineages perpetuated through maternal germ cells, can exhibit different patterns of phylogenetic relationships from the populations of organisms in which they reside (Neigel and Avise 1986).

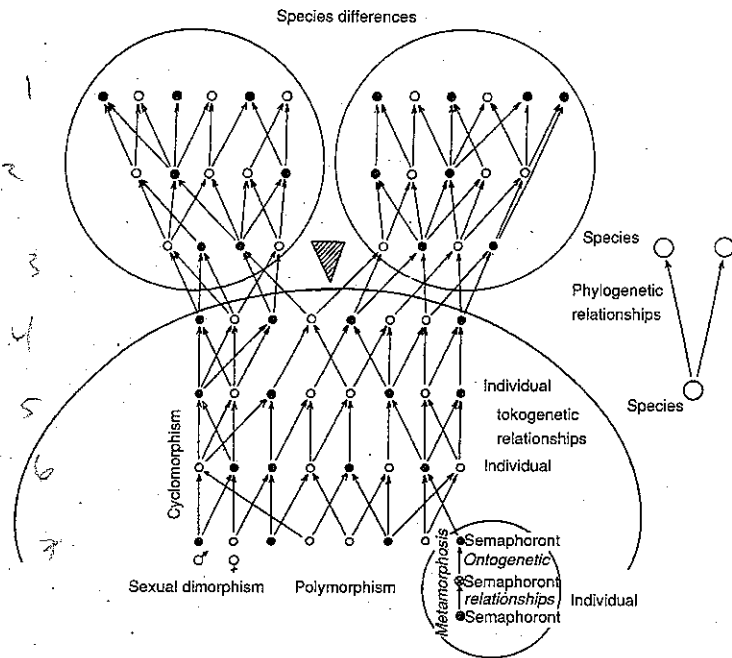


Fig. 15.3. The total structure of hologenetic relationships and the differences in form associated with its individual parts. After Hennig 1966: 31, fig. 66. Reprinted with the permission of University of Illinois Press.

unequivocally phylogenetic relationships on the one hand and the ontogenetic relationships on the other', and that 'this area naturally corresponds to the species category of organisms with bisexual reproduction' (Hennig 1966: 44).

Hennig's discussion of hologenetic relationships in sexual organisms is insightful, as is his recognition that the difference between reproduction and development is not always entirely clear in the case of asexual organisms (cf. Janzen 1977 and the 'genet'/'ramet' terminology of botanists, e.g. Harper 1977). Nevertheless, we disagree with his views on the status of asexual 'species' and the limits of their phylogenetic relationships. In asexual organisms tokogenetic relationships have a fundamentally different structure than they do in sexual forms, each organism being the direct descendant of one, rather than two parents. In such cases there are no systems deriving their existence from interbreeding as there are in sexually

reproducing organisms. Consequently, in obligately asexual groups, phylogenetic relationships correspond precisely with tokogenetic relationships, both being relationships among individual organisms (i.e. life cycles *sensu* Bonner 1974).

SPECIES

If we endeavour to practise systematics in the sense of Griffiths, then species names (or the names of any systematic taxa) should refer to the individual members of one of the classes of entities that exist as the outcome of some natural process. But this still leaves open different possibilities, because distinct classes of entities relevant to phylogenetic systematics derive their existence from both interbreeding and common descent.

We will illustrate these possibilities with a hypothetical situation. Suppose that we have identified all of the separate populations within a particular monophyletic group and that the phylogenetic relationships among these populations have been assessed using cladistic methods (Fig. 15.4). In actuality, the relationships might be more completely resolved than those shown in Figure 15.4, but for the sake of the following discussion we

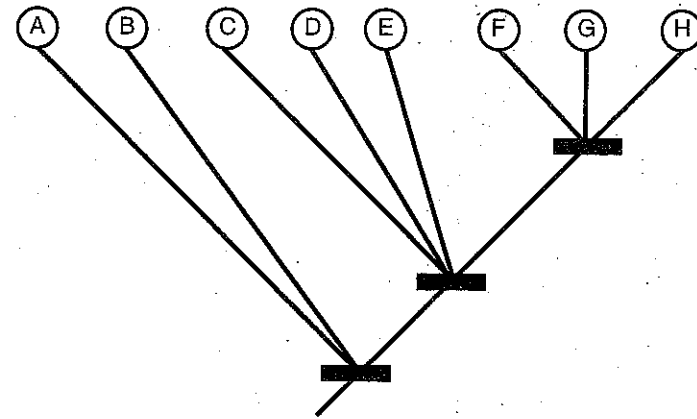


Fig. 15.4. A cladogram of eight populations (A-H); interbreeding occurs within each population, but not among populations. Although certain monophyletic groups of populations exist, the populations themselves are not necessarily monophyletic.

will assume that the organisms in some of the populations are not differentiated from one another, and therefore some relationships cannot be resolved. Indeed, we expect that cladograms of populations will often be less than fully resolved (Arnold 1981, Donoghue 1985; also see discussion below of direct ancestry under 'Species Concepts Based on Monophyly'). This case provides a framework for considering several possibilities for the application of the term 'species'. We will use it to illustrate the consequences of adopting each of several alternative species concepts. It is not our intent, however, to advocate one of these concepts over the others. Instead, we accept the validity of each one and explore its implications for phylogenetic systematics and taxonomic conventions.

Species Concepts Based on Interbreeding

One possibility, which might be considered even without any knowledge of cladistic relationships, would be to apply species names to each of the eight separate populations (A-H, Fig. 15.4). This alternative focuses on the systems that exist as a result of interbreeding at the present time, without considering what might happen to them in the future or their phylogenetic relationships to one another. In effect, this is a narrow version of the biological species concept.

Equating species with actually interbreeding groups of organisms would be useful to many biologists, since these entities are presumed to play a special role in the evolutionary process (e.g. Futuyma 1986). Furthermore, the entities recognized as species under this concept are significant from the perspective of phylogenetic systematics, since, as we argued above, populations are the least inclusive units appropriate for use as terminal taxa when analysing phylogenetic relationships among sexually reproducing organisms.

In view of the fact that populations are not always monophyletic, this concept might appear to entail a double standard concerning the criterion of monophyly. This is not the case. In keeping with the tradition in which species are seen as fundamentally different from other taxa, the names of species simply would designate an entirely different kind of entity than the names of other taxa in the phylogenetic system (de Queiroz 1988). The 'higher' taxa, as systems of common ancestry, would be members of the category 'monophyletic group', but members of the species category, as interbreeding systems, might not be monophyletic. In short, there would be two different classes of systems formally recognized as taxa. That groups of actually interbreeding organisms are not always monophyletic is not, by itself, a reason to avoid designating such groups as species; evolu-

tionary descent is not the only process through which organisms are related, nor is monophyly the only form of existence.

Perhaps the main difficulties with this species concept are practical ones. It is often very difficult to determine the limits of actual interbreeding, especially since the degree of gene flow varies in space and time, and there need be no correspondence between interbreeding and morphological or ecological divergence (Mishler and Donoghue 1982, Donoghue 1985). Beyond this methodological problem, adoption of this concept would probably lead to conflicts with traditional species taxa. If species names were applied to all separate populations, there would be many more species than are currently recognized. Furthermore, organisms that reproduce exclusively by asexual means could not be considered to be parts of species.

There is a well-known alternative to applying species names to actually interbreeding groups of organisms: namely, to have species names represent potentially interbreeding groups of organisms—the broad (and standard) version of the biological species concept. This alternative is conceptually related to the first, and because there is presumably a continuum of reproductive interactions—from frequent to rare to none at all—these two concepts grade into one another.

In order to explore this alternative, suppose that in addition to the information represented in Figure 15.4 we also know the potential of organisms in each of the eight populations to interbreed with one another and produce fertile offspring. In particular, suppose that members of populations A-E can successfully interbreed (even though they are not actually interbreeding), and that members of populations F-H also can interbreed among themselves, but that interbreeding is not possible between organisms from the two different groups of populations (Fig. 15.5). If the species category is defined on the basis of the potential to interbreed, then species names would be given to these two groups of populations (A-E and F-H).

Delimiting species on the basis of the potential to interbreed is appealing, in that it attempts to capture the idea that species exist through evolutionary time rather than being manifestations of current gene flow. Moreover, loss of the potential to interbreed guarantees that the entities are functioning as separate evolutionary units. In these respects, the potentially interbreeding species concept is similar to the evolutionary species concepts of Simpson (1961) and Wiley (1978), which emphasize the existence of species through time by viewing them in terms of their fates as lineages. One might argue, for example, that populations among which there is potential but currently no actual interbreeding might come back in

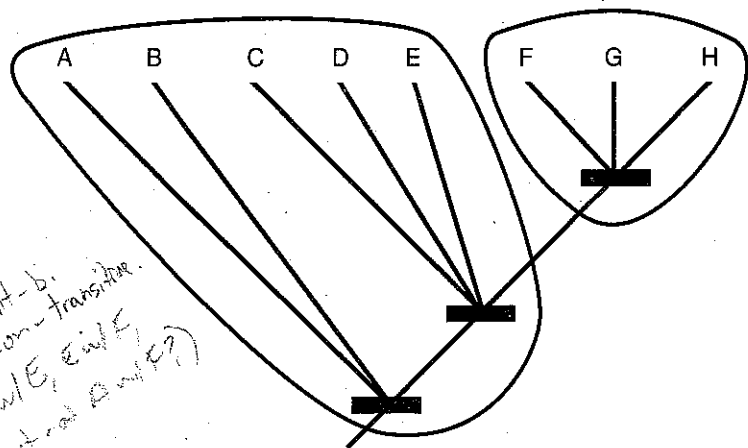


FIG. 15.5. A cladogram of separate populations (as in Fig. 15.4) showing potentially interbreeding groups. Organisms within the enclosed groups of populations (A-E and F-H) can potentially interbreed; interbreeding is not possible between organisms from the different groups.

contact in the near future, at which time there would be sufficient gene flow that the populations would fuse, and any differentiation between them would disappear. In other words, given enough time, these populations would be in contact often enough that they would function together as a single unit in evolution.

Despite this appeal, defining the species category in terms of potential interbreeding also has theoretical drawbacks. Units recognized strictly on this basis need not be, and perhaps often will not be, cohesive in the short run or even in the long run. Species based on potential interbreeding may be simply collections or classes, the members of which are functioning and will always function as separate units in the evolutionary process. Consequently, the processes responsible for 'speciation' (i.e. irreversible reproductive closure) under this concept are not necessarily the same as those responsible for the origin of separate evolutionary units. Furthermore, as noted earlier, potentially interbreeding groups defined solely by the retained ability to interbreed might be paraphyletic; in other words, they might not be systems of common ancestry any more than interbreeding systems. Such demonstrably paraphyletic groups (e.g. populations A-E in Fig. 15.5) obscure information on common ancestry, which in turn hinders

the study of historical biogeography and character evolution. It is not clear how the recognition of such units, which are neither cohesive nor monophyletic, and which are delimited on the basis of what might or might not occur in the future, can be used in testing theories about evolutionary processes (W. Maddison in Vlijm 1986).

Potential interbreeding as a criterion for circumscribing species has practical advantages over the first alternative, because it avoids the technically difficult task of assessing which organisms are actually interbreeding with one another. Furthermore, in contrast to giving species names to populations, it probably would not greatly increase the number of species now recognized, and might even substantially reduce the number in some groups. Nevertheless, defining the species category in terms of potential interbreeding is plagued by its own practical difficulties, particularly when it is viewed as an attempt to identify separately evolving lineages. It is, after all, difficult to determine which organisms will and will not be able to interbreed successfully on the basis of morphological, behavioural, or ecological similarities and differences, and the results of laboratory experiments cannot always be extrapolated to natural circumstances. But even if these problems could be solved, it still would be difficult, if not impossible, to predict future developments such as the duration of persistence of potential interbreeding or changes in geographic ranges that might bring populations into contact. Information about such developments must be available if separately evolving lineages are to be identified accurately, and to the extent that the future cannot be predicted, lineage concepts of species can only be applied retrospectively.⁵

Species Concepts Based on Monophyly

A second set of possibilities focus on evolutionary descent. Here species taxa are some subset of those groups thought to be monophyletic, whether or not they are cohesive. Thus, species would be systems of the same sort as 'higher' taxa in the phylogenetic system, and the species category would designate one rank in a hierarchy, all the ranks of which would be applied to monophyletic taxa. The process of delimiting such species might proceed as before, with the identification of appropriate basal units (populations in the case of sexually reproducing organisms) and the assessment of phylogenetic relationships among them (Fig. 15.4). Under the requirement

⁵ Throughout this essay, 'lineage' refers to a single ancestor-descendant sequence, and is not to be equated with 'monophyletic group'. Monophyletic groups are often composed of multiple lineages (de Queiroz 1988).

can potential int-b. ever be non-transitive. (e.g. A and E, E and F, but not A and F?)

US, P&G, 1-3

(Isn't this the same prob. you dismissed on 334-5?)

(can't we rather take this as evidence that sometimes box IV (p. 327) is useful?)

or

can

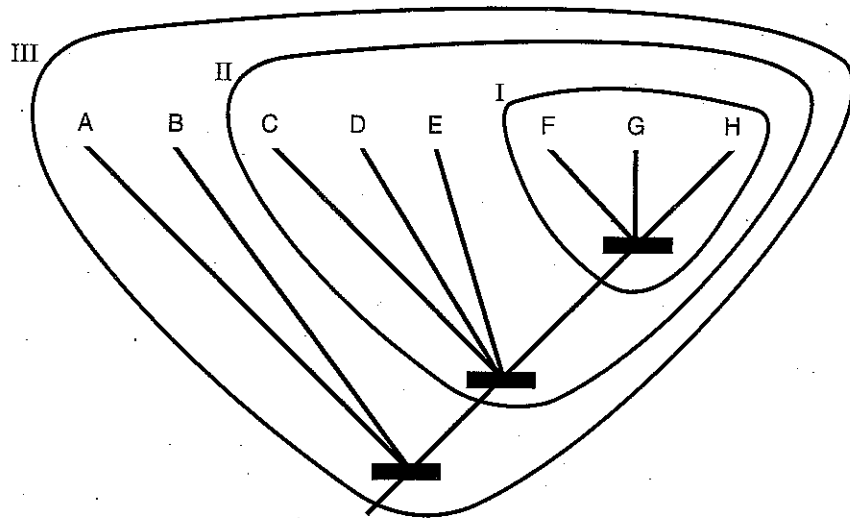


Fig. 15.6. A cladogram of separate populations (as in Fig. 15.4) showing three monophyletic groups of populations (I–III).

that all taxa, including species, be monophyletic groups, the groups labelled I, II, and III in Figure 15.6 would qualify. But which one(s) of these monophyletic groups ought to be assigned to the species category?

One possibility is to recognize as species all and only the smallest (least inclusive) monophyletic groups—either individual populations or groups of populations. In our example, the clade labelled I would therefore be recognized as a species, but clades II and III could not be species for at least two reasons. First, they are not the smallest monophyletic groups, and second, recognizing one or both of them (as well as clade I) as species would result in species nested within one another, which would take away the meaning of categorical ranks altogether. Thus, if clade I is a species, then clades II and III must be 'higher' taxa, in which case the lowest-ranking monophyletic taxon to which any of the populations A–E could be assigned would be a 'higher' taxon. In short, it will be possible to assign all organisms/interbreeding populations to one or more monophyletic taxa, but it will not be possible to assign all such entities to monophyletic taxa of species rank.

This conclusion is not simply a function of having chosen at the outset to recognize only the smallest monophyletic groups as species; the same

result obtains even when more inclusive monophyletic groups are recognized as species. For example, we might choose to recognize clade II as a species, but then it would not be possible to assign populations A and B to a monophyletic taxon of the species category. Neither does the problem result from incomplete information about phylogeny, for some population(s) may be ancestral to others, and hence paraphyletic. Although identification of ancestral populations is generally a difficult task, such populations presumably exist. Even if their status as direct ancestors cannot be demonstrated, they are likely to appear in cladograms as parts of unresolved polytomies or as single branches without diagnostic apomorphies.

Although not assigning all organisms or populations to taxa of species rank violates a long-standing convention, this alone is insufficient grounds for rejecting a definition of the species category based on monophyly. If the goal of systematics is to depict relationships accurately, then any traditions that interfere with this goal should be abandoned.

There is, however, a way of emphasizing monophyly in the definition of the species category while also providing for the assignment of the vast majority of organisms to species taxa. This is achieved by introducing a convention that allows the recognition as species of single basal entities, or groups of basal entities, whose monophyletic status is uncertain (Donoghue 1985). For example, the relationships of populations C, D, and E in Figure 15.4 are unclear. Together they may form a monophyletic group, or this group may be a paraphyletic assemblage—characters support neither hypothesis (Fig. 15.7). Following Donoghue (1985) and Gauthier *et al.* (1988), potential paraphyly should be distinguished from demonstrated paraphyly, in which there is evidence that some populations are more closely related to populations placed in another taxon. Demonstrably, paraphyletic groups would not be recognized as taxa under this convention. Nevertheless, the following kinds of groups might be recognized temporarily on the grounds that they may be monophyletic: (1) populations lacking autapomorphies, or (2) groups of populations that are not differentiated from one another and that lack the diagnostic apomorphies of any clade(s) nested within the least inclusive monophyletic group to which they belong (e.g. the group of populations [C, D, E] in Fig. 15.6). If this proposal were adopted, it might be desirable to give such groups of uncertain status a special designation (Donoghue (1985) proposed 'metaspecies', and suggested that their names be marked with an asterisk). These measures are intended to ensure that such taxa would be treated cautiously until their relationships are better understood. The 'metaspecies' convention allows an unambiguous reflection of phylogenetic

So A
was not
even be
part of
a
species?
That
seems
insane!

Seems
pretty
obvious
though!

ok but
I'd rather
not put
it in
the
book

but
can't
we just
even
do an
H. im
H. im
H. im
own
species?

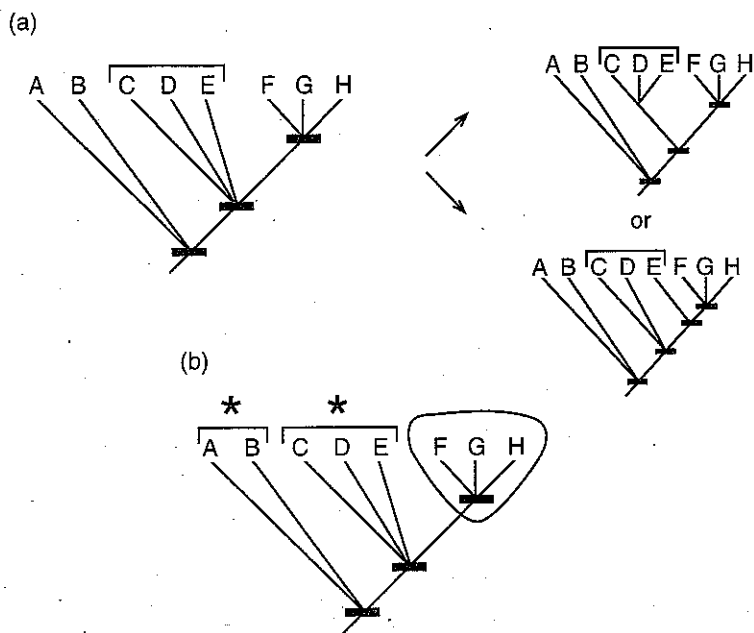


Fig. 15.7. Cladogram of populations (as in Fig. 15.4). (a) Possible resolutions of the unresolved group of populations C-E. In the upper resolution, C-E is found to be monophyletic; in the lower resolution, C-E is found to be 'positively' paraphyletic. (b) Application of the 'metaspecies' convention, where asterisks symbolize metaspecies A-B and C-E; populations F-H form a 'positively' monophyletic species.

relationships, in so far as these are known, while also allowing unresolved groups of organisms to be assigned to taxa of species rank.

Nevertheless, if the criterion of monophyly is to be applied consistently to basal entities as well as to groups of such entities, then it still would not be possible to recognize as species (or monophyletic taxa of any rank) populations that are known to be ancestral to others (perhaps through direct observation of an immigrant establishing a new population). Such populations are paraphyletic (although not necessarily as evidenced by characters), and therefore would not be covered by the metaspecies convention, because they contradict the fundamental idea of a species concept based on monophyly. As pointed out by Hennig (1966: 71), an ancestral species, before it gives rise to any descendants, is equivalent (as a mono-

phyletic group) to the group composed of itself and all the species descended from it considered at a later time. Thus, the ancestral population of a monophyletic group recognized as a genus is part of that genus but not of any less inclusive monophyletic taxon. Nevertheless, given the difficulty of identifying ancestors (Wiley 1981), leaving these unassigned to taxa of species rank is unlikely to cause great practical problems.

The case in which 'species' refers to the least inclusive monophyletic groups has several other practical difficulties. One problem is that it is not an easy task to construct cladograms using populations (or organisms) as terminal units (cf. Arnold 1981), and this degree of resolution is far from being achieved in most groups. Another problem is that there would probably be more species recognized if this approach were adopted than we are presently accustomed to; for example, many groups that are presently accorded subspecific ranks would qualify as species (Cracraft 1983). In asexual organisms the situation would be even more extreme.

A more general objection to defining the species category as one level in the hierarchy of monophyletic groups arises from considering the usefulness of categorical ranks. Linnaean taxonomy requires two distinct activities: grouping, the discovery/identification of groups, and ranking, the assignment of a Linnaean categorical rank to each one of these groups (Donoghue 1985).⁶ In systematics (*sensu* Griffiths), the activity of grouping corresponds with systematization itself, but the significance of ranking is less clear. Although monophyletic taxa exhibit a nested, hierarchical pattern of relationships, which is exactly the same kind of pattern used in Linnaean taxonomies, categorical ranks add no information about monophyly that is not already contained in a cladogram or an indented taxonomy (Eldredge and Cracraft 1980; Gauthier *et al.* 1988).

There is also the problem that the very existence of categorical ranks encourages spurious comparisons between entities assigned the same rank but that are not otherwise comparable (Gauthier *et al.* 1988). One possible solution to this problem is to have ranks reflect the absolute ages of groups (Hennig 1966), but this proposition has not been accepted by most systematists. Another possibility suggested by Hennig (1969) and Griffiths (1974, 1976), among others, is that the categorical ranks of Linnaean taxonomy be abandoned. If ranking serves no purpose other than perpetuating

⁶ The term 'grouping' is unfortunate, in that it seemingly implies that the 'groups' are formed by some human activity, rather than existing independently and being discovered by humans. Furthermore, the term 'group' itself, as in 'monophyletic group' and 'historical group', is unfortunate, in that it seems to imply that such entities are collections rather than more inclusive wholes. At best, such usage reflects viewing the whole not from its own level but from the level of the less inclusive entities (parts) of which it is composed.

tradition, the difficulties associated with it provide a compelling reason for considering the possibility of abandoning ranks.

It is ironic that the possibility of eliminating ranks, which arose from considering 'species', like other taxa, to be monophyletic groups, reopens the alternative of a species concept based on interbreeding. If 'species' simply denotes one hierarchical rank within the category 'monophyletic group', and if ranks are unnecessary, then why should some monophyletic groups be called 'species'? In other words, while the abandonment of categorial ranks in no way hinders the representation of monophyletic groups, it also frees the term 'species' to represent some other, entirely different category. And, if freed in this way, why not use the term to designate some kind of interbreeding group?

A Disjunctive Species Concept

An alternative to species concepts based on interbreeding, as well as those based on common descent, is to base the concept on both of these processes—a disjunctive definition of the species category (cf. Hull 1965, Løvtrup 1987). Under such a concept, species *either* would be populations (whether monophyletic or not), *or* they would be monophyletic (but not para- or polyphyletic) groups of populations. This alternative allows all populations/organisms to be assigned to species-level taxa. It has other implications as well. *First*, to the extent that only populations are recognized as species in sexually reproducing groups, it converges on the approach of recognizing every separate population as a species. *Second*, some 'species' would be different kinds of entities than other 'species', as well as taxa at other levels in the phylogenetic system. From the viewpoint of cladistic analysis, these considerations may seem unimportant, because both populations and monophyletic groups are appropriate terminal taxa. In any case, this problem could be remedied by introducing a new set of conventions (along the lines of 'metaspecies') to distinguish these different kinds of entities from one another. However, in view of the confusion that might be generated by mixing the processes of interbreeding and common descent, a disjunctive definition may create more problems than it solves, especially if its only benefit is maintaining the tradition of assigning all populations/organisms to taxa of the species category.

CONCLUSIONS

Our analysis implies that neither populations nor monophyletic groups are generally more real or significant than the other; instead, their relative

significance varies with the particular theoretical context. We therefore agree with the tenet that '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 organisms' (Kitcher 1984: 309). Nevertheless, we reject the brand of pluralism that applies different criteria or even different combinations of criteria on a case-by-case (group-by-group) basis in an attempt to achieve a single, optimal, general-purpose taxonomy. Attempting to reflect a combination of processes, so as to provide species taxa significant in all contexts, will only result in confusion over what species taxa represent, and how they might be used.

From the viewpoint of phylogenetic systematics, each of the species concepts we have considered designates units that can be used as terminal taxa, and each one also has consequences. Disjunctive species concepts, because they mix different classes of systems, result in species taxa that are not comparable. Such concepts are at odds with the unambiguous representation of different kinds of systems. Species concepts based on interbreeding entail the absence of species in organisms that reproduce only asexually. Within this category of species concepts, potentially interbreeding groups of organisms may be neither monophyletic nor cohesive; that is, they may not represent unitary evolutionary entities, and they may exhibit cladistic relationships among their included populations. Species concepts based on actual interbreeding may result in recognizing as separate 'species' entities that over longer time periods function together as a single evolutionary unit. Finally, if all species are to be monophyletic, then some organisms are not parts of species, although in contrast with species concepts based on interbreeding, these organisms are not asexuals but members of ancestral populations.

In considering these consequences, a given reader may see some as insurmountable difficulties and others as simple facts of life. However, which consequences are viewed as problems and which ones as facts will differ, depending on one's point of view. This is the species problem. Given this state of affairs, we can imagine several possible fates for the term 'species'. One possibility is that it may become restricted to one of the classes of real biological entities, such as those resulting from interbreeding or those resulting from common descent. Which of these concepts is favoured depends not only on the theoretical context but also on whether 'species' is viewed as the name of a class of real biological entities or as the name of a rank in a hierarchy within a class of real biological entities. Alternatively, 'species' may continue to be used as a general term referring to an assemblage of several classes sharing nothing more than having been conflated historically. Realistically, the use of the term 'species' will be determined as much by historical and sociological factors as by logic and

biological considerations. In any case, the entities deriving their existence from different natural process are all valid objects of investigation. Acknowledging this fact and exploring the relations among the different kinds of entities is central to both biology and systematics.⁷

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