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A Critique of the Biological Species Concept and Recommendations for a Phylogenetic Alternative

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Abstract. *Discussions that have accompanied biological species definitions often imply correspondence between breeding groups and morphological and ecological units. It is often assumed that the cause of such correspondences is gene flow or the lack of it. This has generated confusion because breeding, morphology, and ecology can be, and often are, uncoupled, and the effects of gene flow may be limited. Another source of confusion has been the failure to distinguish clearly between species themselves (taxa) and concepts of the species category. The biological concept fails to provide unambiguous criteria for grouping organisms (or for assigning species rank), and as a consequence, biological species may not be monophyletic. A phylogenetic species concept, which emphasizes monophyly, is more appropriate for purposes of phylogeny reconstruction, cladistic classification, and the study of evolutionary processes.*

Why is it that the word “species” is still so problematical? Why haven’t biologists, or at least systematic biologists, been able to agree upon a single concept and definition? A popular answer is that patterns of variation are so diverse and complex that no one concept or definition can suffice (e.g., Davis & Heywood 1963; Dobzhansky 1972; Sokal 1973). A related response involves the process of evolution. If descent with modification occurs—if new forms arise from older ones more or less gradually—then difficult cases should be expected (e.g., Dobzhansky 1937).

These standard responses are surely correct, but there are other reasons why controversies persist. There are, for example, disagreements over basic philosophical issues, such as the nature of reality. Many biologists and some philosophers argue that organisms are real but that species are not. Species, then, are constructs of the human mind, mere inventions (e.g., Darwin 1859; Haldane 1956; Levin 1979). Others contend that species really exist and are not arbitrary and that they must exist if evolution works the way we think it does (e.g., Mayr 1963; Eldredge & Cracraft 1980). These same individuals often insist that categories above or below the level of species are subjectively defined—necessary perhaps, but arbitrary.

There is also the question whether particular species are (or should be considered) natural kinds—“classes” with one or more defining characteristics—or as “individuals” without defining traits but with unique origins, spatio-temporal existences, and internal cohesion (e.g., contrast Ghiselin 1974 and Hull 1976, 1978 with Caplan 1980, 1981, and Ruse 1981). If particular species are classes, it would be

appropriate to formulate theories about them. On the other hand if species are individuals, then theories about them would be inappropriate, although we might still construct theories about the class of all species. These questions may appear abstract, yet answers to them may have profound effects on the theory and practice of not only systematics and evolutionary biology (Hull 1980; Beatty 1982), but of philosophy, psychology, linguistics, and other disciplines as well (Ghiselin 1981). Fortunately, these issues are now being discussed actively.

There are still other sources of confusion that have received insufficient attention. Because concepts and definitions have not always been formulated clearly or because these are linked to theories that are problematical, we sometimes fail to make important distinctions between ideas and phenomena that should be clearly separated in our minds. Concepts and definitions that are fraught with such internal difficulties confound the study of evolution. Sometimes a concept or definition may become more a source of confusion than an aid to understanding, and in such cases the best solution may be to abandon it altogether. My objective in this paper is to discuss several sources of confusion that I think have been perpetuated by the biological species concept and to recommend ways that confusion might be avoided. I will also outline an alternative species concept developed recently by de Queiroz et al. (MS in prep.).

The biological species concept provides a good example of two general sources of confusion. The first concerns correlations and causes and the second the distinction between grouping and ranking. Although these problems are not restricted to the bi-

ological concept, this concept is especially well suited for my purposes because it is widely known and has been explicitly formulated. However, the biological species concept has been discussed and criticized so much in the past that some additional justification is required before undertaking yet another critique, particularly since most botanists (and many zoologists) have long since abandoned it! While most criticisms of the biological concept have been concerned primarily with its practicality (e.g., Sokal & Crovello 1970; Cronquist 1978), and indeed, I suspect many biologists have simply rejected it as non-operational, my concerns are very different. I am not especially concerned with whether the biological species definition is workable (in this I agree with Hull 1968), but instead with whether it is a good idea and if it has been formulated clearly enough. Also, I believe that confusions wrought by the biological concept are still very much alive. One possible objection to a critique of the biological concept is that criticisms are being directed at a straw man—a crude or outdated version of the concept. Because I am trying to pinpoint general confusions (confusions that transcend any one concept) this concern is not overly important here. However, I do wish to make some substantive comments about the biological concept and for this purpose will concentrate on Mayr's account of 1982.

CORRELATIONS AND CAUSES

I begin with my principal conclusions and then set out arguments to support them. If a concept (or definition) assumes correlations or implies correspondences between things that can and do vary independently, then it is very likely to generate confusion. I think that the biological species concept has caused confusion by implying close correspondence between breeding groups and morphologically and ecologically distinct groups, when these groups often do not correspond. I also suggest that if a concept (or definition) is tied to a theory of causation that turns out to be ill-founded, then continued use of the concept will retard progress toward a better causal theory. The biological species concept rests on the idea that interbreeding (or the inability to breed) is of prime importance in evolution, i.e., breeding determines whether morphological or ecological divergence can occur. This theory now appears grossly oversimplified and, as a result, so does the biological species concept. I submit that the biological species concept is currently doing more harm than good and that it should be either substantially revised or abandoned entirely.

These assertions could be dismissed by pointing out that, strictly speaking, most biological species definitions given by Mayr and others involve breed-

ing alone and do not specify directly any correlations or causes. But there is much more to the biological species *concept* than any one definition. The discussions that have accompanied the definitions over the years are an integral part of the concept—they clarify the intent and significance of the definitions and have exerted a more profound influence on the theory and practice of systematics than the definitions themselves. In any case, regardless of the exact wording of the definitions, it is clear that in practice correspondences between units are commonly assumed, and it is generally taken for granted that breeding is of utmost importance.

It may clarify my position to consider the motivations and development of the biological concept. This is an enormously complex issue and what follows is but one analysis of the context of development of the concept. For an alternative account and for many additional references to original literature the reader should consult Mayr (1957, 1982).

It has long been clear that at any one place and time there are morphologically distinct groups of organisms (populations) that do not intergrade (Mayr's "nondimensional species"). In group after group taxonomists demonstrated that variation was discontinuous and that organisms did not intergrade insensibly but instead were separated by gaps—by imaginable combinations of characters that did not exist (Dobzhansky 1937). To be sure, this became less clear-cut when one considered closely related organisms and/or moved about in space or time, but even then distinct morphological units seemed to exist (e.g., Gould 1982).

These very basic observations about the nature of morphological variation called for some explanation, and several causal theories were advanced. Early explanations were non-evolutionary and typological. Variation within each basic kind was attributed to the imperfect manifestation of its underlying essence. Alternative accounts derived from observed correlations between morphology and other attributes. Breeding was identified as one common correlate even by early naturalists. It was recognized that members of the same morphological unit at one time and place could interbreed, but that members of different units could not. At first this observation was incorporated into non-evolutionary explanations—the ability to interbreed was taken as evidence of genealogical descent from the first representatives of each separately created type (e.g., see Mayr 1982: 257, for discussion of Cuvier). Several early naturalists suggested that breeding be used to test whether organisms with distinct appearances (perhaps, for example, males and females) should be placed in the same or in separate species. If two organisms were offspring of the same parent or could interbreed freely they were to be considered con-

specific. Buffon, in the mid-1700s, was perhaps the first to suggest using breeding as a criterion both for deciding whether organisms with very different appearances should be placed in the same species and whether similar organisms should be assigned to different species (Mayr 1982: 260–263).

The modern biological species concept seems to have developed out of observed correlations between breeding and morphology in some groups of organisms and from the idea that breeding could be used as a test of species status in difficult cases. With the rise of genetics, especially population genetics during the early 1900s, it seemed by the late 1930s appropriate and safe to assume that the exchange of genes was of prime importance in evolution (Mayr & Provine 1980). In my view the biological species concept was one very significant manifestation of this idea. It effectively turned the presumed relationship between breeding and morphology into a theory of cause and effect. Mayr (1963: 31) was very clear about this:

The argument of proponents of the morphological species concept runs about as follows: "Natural populations considered by general consent to be species are morphologically distinct. Morphological distinctness is thus the decisive criterion of species rank. Consequently, any natural population that is morphologically distinct must be recognized as a separate species." The conclusion is fallacious, even though based on the correct observation of a general correlation between reproductive isolation and morphological difference. It is fallacious because it overlooks the strictly secondary role of morphological differences. The primary criterion of species rank of a natural population is reproductive isolation. The degree of morphological difference displayed by a natural population is a by-product of the genetic discontinuity resulting from reproductive isolation.

In this view organisms remain similar because they interbreed often enough, and distinct morphological units arise and are maintained by barriers to interbreeding. Reproductive isolation insures the integrity of well-adapted genomes. Given this theory of cause and effect, it seems only natural to define species in terms of their primary cause (breeding) rather than in terms of some incidental effect (morphology or ecology). In those (presumably few) cases in which the fit between morphology and breeding is inexact, breeding should be given primacy on account of its supposed overriding importance.

According to the interpretation I have just outlined, the biological definition of species was a natural outcome of the biological species concept (for a similar account see Davis & Heywood 1963). This development seems reasonable—it is not wrong to advance a causal theory based upon observed correlations, and definitions of key terms should be brought in line with causal theory. However, when

a theory is advanced it should be tested. Unfortunately, the biological concept was not critically examined before correspondences between morphological, ecological, and breeding units were assumed, and the primacy of gene flow was accepted as obvious. Generalizations were quickly extended from a very few organisms to virtually all organisms, and observations of non-correspondence were brushed aside as rare exceptions or as evolutionarily insignificant (for recent examples, see White 1978).

It was not long before Mayr and others, recognizing the practical difficulties of determining directly the limits of interbreeding groups, suggested using morphological and ecological criteria as evidence for the existence of biological species (e.g., Mayr 1969: 28–29). Thus gaps in morphology provided evidence of reproductive isolation, and similarities in morphology were taken as evidence of actual interbreeding. Confident of the existence of a general correspondence, the presumed effects (morphology and ecology) could be used to indicate the limits of breeding units. An extension of this reasoning is evident in the implication that the match between folk taxonomies and modern species classifications demonstrates the existence of biological species (Diamond 1966; Gould 1979). This, however, does not follow logically. Modern species delimitation is, in almost all cases, still based upon morphology and geography and not upon direct knowledge of breeding behavior. If folk and modern classifications really do match (and this seems questionable in many cases), this correspondence would at most corroborate the existence of morphologically/ecologically distinct units at one time and place. This has never been at issue.

Although the reasoning just discussed is logically flawed, it would not be a serious source of confusion if (1) the presumed correlations were indeed common, and (2) if breeding were primary in causing or preventing morphological or ecological change. Unfortunately, as discussed in the remainder of this section, the situation on both counts now appears to be more complex than it seemed initially (see Mishler & Donoghue 1982, for more detailed discussion and additional references).

Evidence has steadily accumulated since the publication of Ehrlich and Raven's paper (1969) documenting the very small size of actually interbreeding groups in many kinds of organisms (Levin & Kerster 1974; Grant 1980; Levin 1981). Effective gene flow can be very limited even when extrapolated over long periods of time, and thus there may be many separate interbreeding groups within recognizable morphological or ecological units. It is also clear that potentially interbreeding groups do not necessarily correspond to morphological or eco-

logical units. Thus, in the case of “sibling species,” there may be several reproductively isolated units within morphological species. In other cases reproductively isolated units are extensive and include numerous morphological and/or ecological units. The genus *Quercus*, wherein the potentially interbreeding units correspond to entire subgenera (Burger 1975; Van Valen 1976), provides a well-known example of a phenomenon that is undoubtedly very common in plants (Grant 1981).

It also appears now that “ecological units”—however these might be defined—often do not correspond well to breeding or morphological units. Thus, as the experiments of Turesson (1922), Clausen et al. (1940), and many physiological ecologists since then have demonstrated, there may be numerous ecologically distinct variants within what would normally be considered morphological or biological species.

It is now also recognized that selection can sometimes result in morphological and/or ecological divergence even in the face of considerable gene flow (Endler 1977). A well-studied natural instance of such “diversifying selection” involved grass populations on mine tailings (Jain & Bradshaw 1966; Antonovics 1972). It also seems that stabilizing selection and/or developmental homeostasis (and perhaps other factors) can have the opposite effect, that is, can maintain similarities in morphology for long periods even when populations are separated by very great distances and interbreeding is impossible (Levin 1979; Van Valen 1982).

These observations lead to the conclusion that there are no necessary correspondences between ecological, morphological, and breeding units, and that non-correspondences are common. Moreover, the role of interbreeding and the role of barriers to interbreeding in preventing or allowing morphological or ecological change now seem questionable in many cases (Levin 1978, 1979). To the extent that the biological species concept implies otherwise, it will only delay a better understanding of the necessary and sufficient causes of evolutionary change. Given what we now know about patterns of variation and the evolutionary process, we must develop a species concept that incorporates the observation that breeding, morphology, and ecology are not necessarily linked, and insists that the nature of the correspondences between these be detailed in each case. A better species concept would not be wedded to the theory that gene exchange is of overriding importance in evolution. Instead, as discussed below, it might best be tied to a more general and less controversial theory, namely that evolution occurs and produces a hierarchy of monophyletic groups.

GROUPING AND RANKING

Another confusion perpetuated by the biological species concept, which has not been as obvious as those discussed above, is the failure to distinguish clearly between groups (taxa) and ranks (categories), and the associated failure to specify criteria for placing organisms into groups as distinct from criteria for assigning groups to particular ranks in the hierarchy. In this section I will argue that when the biological species definition is applied, grouping and ranking take place simultaneously—there is, in effect, only one criterion. As a consequence, application of the biological definition can lead to the recognition of non-monophyletic species—taxa that should be unacceptable to systematists desiring genealogical classifications. This problem can be avoided by clearly specifying separate grouping and ranking criteria and by giving primacy to grouping over ranking.

Confusion over grouping and ranking, like the problems discussed above, has resulted from an incongruence between biological species definitions and the discussions associated with them. It is well-known that Mayr (1942) did not distinguish consistently between species as taxa—actual groups of organisms—and the concept of the species category. This is understandable in hindsight because the distinction was not widely appreciated at the time, and the terminology needed to make it had not yet become popular. Thus as Mayr (1982) has pointed out, the word *taxon*, a general term for groups of any rank, was not introduced until 1926 by Meyer-Abich. Although it was used by some botanists during the 1940s, it was not incorporated into the International Code of Botanical Nomenclature until 1950. Surprisingly, the word *taxon* was not widely adopted by zoologists until even later, mostly after the appearance of Mayr et al.’s systematics textbook in 1953.

In any case owing to analyses by Gregg (1954), Beckner (1959), Simpson (1961), and others, by 1963 Mayr was well aware that some confusion had been generated by his earlier failure to distinguish clearly between taxa and categories. Since then, the differences between taxa and categories and between grouping and ranking have figured prominently in Mayr’s writing. The following passage (1982: 253–254) is representative:

In retrospect it has become evident that great confusion was caused by the application of the term “species” to two fundamentally different logical categories . . . The *species taxon* must be sharply distinguished from the *species category*. The species category is the class, the members of which are species taxa. The particular definition of the species category which an author adopts determines which taxa he must rank as species . . . The

determination of species status is thus a two-step procedure. The first step consists of delimitation of the presumptive species taxon against others and the second is the ranking of the given taxon into the appropriate category, for example, "population," "subspecies," or "species." . . . Most taxonomists, including myself, were confused about this until a few years ago.

I agree with this analysis. Determining species status *is* logically a two-step procedure involving first grouping and then ranking. It follows, I think, that there must be two parts to a complete concept or definition of species (or of any other taxonomic category)—a group-forming criterion and a criterion for assigning rank. Unfortunately, separate criteria for grouping and ranking are not included in biological species definitions and have not been clearly spelled out even in associated discussion.

Consider, for example, Mayr's well-known definition of 1942 (p. 120):

Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.

From this it might be concluded that groups should be formed on the basis of actual or potential interbreeding and that of such groups those that are reproductively isolated from others should be given species rank. This interpretation is supported by additional comments, for example (Mayr 1982: 253):

When a taxonomist first encounters specimens or individuals in nature that he wants to assign to a species, he deals first with a strictly zoological or botanical problem. Are the individuals from a given district members of the same population? He is concerned not with the problem of rank, as in the case of the problem of the species category, but with problems of delimitation. He deals with a given zoological object, let us say snow geese (*Anser caerulescens*), and attempts to determine whether white and blue birds are products of the same gene pool.

But is this reasonable? If by "same gene pool" Mayr means "actually interbreeding," then there is a difficulty in those (presumably common) cases in which the largest actually interbreeding groups are much smaller than the smallest groups that are separated by reproductive isolating mechanisms. In such cases the grouping criterion yields groups to which the ranking criterion does not apply, namely groups that are too small. If we accept that species delimitation is a two-step procedure we must then ensure that the grouping criterion yields at least some groups that can be assigned rank by the ranking criterion.

But perhaps when Mayr says "same gene pool" he really means "potentially interbreeding." If this is the case then the grouping criterion (potential to interbreed) is equivalent to the ranking criterion (reproductive isolation). Grouping and ranking would therefore be one and the same operation.

A similar analysis can be made of other biological species definitions. For example, according to Mayr's version of 1982 (p. 273):

A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.

Here "reproductive community" has taken the place of "actually or potentially interbreeding," but as a grouping criterion this formulation is equally ambiguous, and the same objections hold. The idea of ecological niche has been added, but it is unclear whether niche is supposed to function as a grouping or a ranking criterion or both.

A different interpretation of biological species definitions is possible, namely that they are meant only to provide a ranking criterion and not to specify how organisms should be placed into groups. But if this is the case, it is legitimate to inquire just how groups are to be formed in the first place, and, as I have pointed out, this is not made clear in accompanying discussions. I can only conclude, therefore, that in applications of the biological species concept groups will be formed by application of the ranking criterion.

By now this will seem a tedious argument. Why am I belaboring the point? Is the problem a purely semantic one or has the failure to distinguish two separate criteria been the cause of substantial misunderstanding? In my opinion what at first appears to be only a minor confusion is an important manifestation of an underlying attitude that some systematists would violently oppose. Put simply, the biological species concept is insufficiently concerned with the constitution of groups (taxa). Because grouping and ranking take place simultaneously, biological species may be unacceptable taxa when judged by criteria that some systematists would like to apply. In particular, biological species may be non-monophyletic groups and should therefore be rejected by cladists (Rosen 1979).

This, I think, is a major problem that has not yet been widely appreciated. A monophyletic group in the sense of Hennig (1966) is one that contains all and only the descendants of a particular common ancestor. It is a group wherein every member is more closely related (in a strictly genealogical sense) to every other member than to any organisms classified outside the group. Hennig showed that evidence that a group is monophyletic is provided only by shared derived characters (synapomorphies) and that groups recognized solely on the basis of shared ancestral characters (symplesiomorphies) might not be monophyletic, but paraphyletic or polyphyletic instead (see Wiley 1981, for definitions).

In the application of biological species definitions organisms (or populations) are assembled into groups

on the basis of interbreeding. But the ability to interbreed may be a retained ancestral trait—a symplesiomorphy (Rosen 1978, 1979; Bremer & Wanntorp 1979). Organisms that can interbreed are not necessarily closely related genealogically, but instead may be simply the left-overs after some subgroup evolved a reproductive isolating mechanism. Thus some members of a biological species may actually be more closely related to (i.e., share a more recent common ancestor with) organisms placed in another species than they are to other members of their own species. This is a counter-intuitive idea because we have grown accustomed to viewing interbreeding as a direct measure of relatedness. But, as strange as it may seem, interbreeding logically cannot be used as evidence of strict genealogical relationship.

If one is a cladist, and hence interested in recognizing only monophyletic groups (to the extent that these can be discerned), then the biological species concept is inappropriate. If one is not a cladist but has in mind some criterion other than monophyly by which to evaluate groups (e.g., genetic, morphological, or ecological similarities and differences), application of a biological species definition may also yield unacceptable taxa (e.g., as in *Quercus*, see above). I suggest that a better species definition would clearly specify a grouping criterion and a ranking criterion. In my view grouping should be given primacy over ranking so that strict control can be exercised over group membership. Grouping should be carried out first and the ranking criterion should be used only to choose among acceptable groups.

A PHYLOGENETIC SPECIES CONCEPT

Thus far I have argued that the biological species concept has generated, or has at least perpetuated, several confusions, and I have recommended that it be modified or replaced by a concept that is freer of confusion. In this section I will briefly outline a new species concept—a phylogenetic species concept—that I think is theoretically sound and avoids the confusions discussed above. Elements of this concept have been discussed previously (e.g., Rosen 1978, 1979; Donoghue 1982; Mishler & Donoghue 1982), and de Queiroz et al. (MS in prep.) provide a much more detailed justification and discussion than I am able to present here.

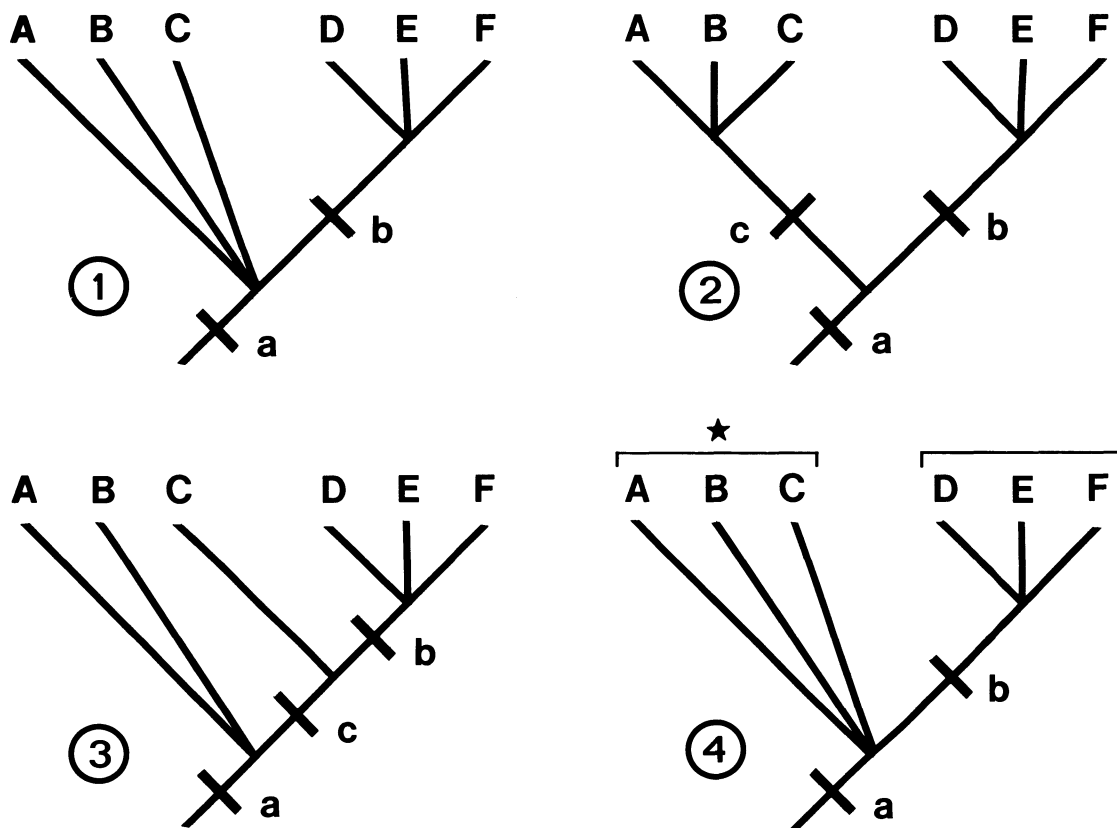
At the outset it is important to recognize that this concept is founded on the conviction that the process of evolution results in a hierarchy of monophyletic groups (*sensu* Hennig, see above) and that classifications should reflect genealogical relationships accurately and unambiguously at all levels and to the limits of our ability to resolve such relation-

ships. Readers who would willingly accept “known” paraphyletic groups in classification will probably not perceive a need for the phylogenetic concept. In my opinion non-monophyletic groups are arbitrary and misleading about character distributions and evolution, but it is not possible here to discuss the relative merits of monophyletic and non-monophyletic groups in detail (see Hennig 1966; Eldredge & Cracraft 1980; Wiley 1981; Nelson & Platnick 1981), and I do not expect others to accept my opinion uncritically. Therefore, I ask only that the reader concede that strictly genealogical classification is a goal of some systematists, and for their purposes at least a new species concept is needed. The following discussion can then be viewed as an exercise in designing an appropriate species concept for this purpose.

If one wishes to resolve phylogenetic relationships as far as possible—to find the smallest monophyletic groups of organisms—then it seems reasonable that individual organisms should be used as terminal taxa in analyzing relationships. However, it is important to stress that by “organism” I mean an entire life cycle. Even though we usually work with single specimens, it is critical to remember that these represent only segments of the life cycle, that is, they are “character-bearing semaphoronts” (Hennig 1966: 6).

Organisms should be placed into more and less inclusive monophyletic groups using shared derived characters as evidence, just as species, genera, or families are united on this basis. Character polarities can be assessed by outgroup analysis (Maddison et al. 1982); this may be especially difficult at the level of organisms, populations, and species (Arnold 1981), but the logic is the same at all levels. It is sometimes claimed that no evidence is needed that species are monophyletic, either because species are monophyletic by definition or because they need not be monophyletic. Although Hennig (1966) and others (e.g., Willmann 1983) restrict the use of monophyly to groups of species, I can see no reason why the concept cannot be and should not be applied more generally to any group at any level that contains all and only the descendants of a common ancestor (de Queiroz et al. MS in prep.).

When I have tried constructing cladograms using organisms as terminal taxa (in the angiosperm genus *Viburnum*), the cladograms obtained have included portions like those shown in Fig. 1–4. In Fig. 1 organisms A–F are united by apomorphy *a* and the subset D–F is considered monophyletic owing to its possession of derived character *b*. But what kind of group is A–C in cladogram 1? Clearly, there is no character evidence that it is a monophyletic group. However, it might actually be monophyletic, and some apomorphic character might eventually be



FIGURES 1-4. Cladograms of the monophyletic group of organisms A-F; a, b, and c represent derived characters. — 1. D-F is a monophyletic group, and A-C is unresolved. — 2. D-F and A-C are both monophyletic groups. 3. — D-F and C-F are monophyletic, A-B is unresolved, and A-C is “positively” paraphyletic. — 4. D-F is a “cladospecies” and A-C is a “metaspecies.” See text for additional explanation.

discovered to corroborate this (e.g., character c in Fig. 2). Thus, in Fig. 1 we can only say that there is no “positive” character evidence that A-C is a monophyletic group.

Many cladists would label A-C in Fig. 1 a paraphyletic group because it can be recognized only by the absence (or the ancestral condition) of character b. But in my opinion, and for purposes of the phylogenetic species concept, it is very important to distinguish the condition of A-C in Fig. 1, which I will call “unresolved,” from the condition of A-C in Fig. 3, which I will call paraphyletic or, more specifically, “positively paraphyletic.” In Fig. 1 all that we can say is that A-C is unresolved. It might be monophyletic or it might be paraphyletic—we simply lack evidence one way or the other. On the other hand in Fig. 3 we have some positive character evidence (apomorphy c) that A-C is not monophyletic, that a part of it (C) is actually more closely related to another group (D-F).

Having made this distinction, I can now state the grouping criterion of the phylogenetic species concept. According to the phylogenetic concept only

monophyletic groups are acceptable; “positively” para- or polyphyletic groups are not. Unresolved groups such as A-C in Fig. 1, which consist of organisms that cannot be consistently distinguished from one another on the basis of heritable apomorphic characters, are acceptable—these are temporarily given the benefit of the doubt. However, if it is discovered that such a group is positively paraphyletic, it must be abandoned. Thus A-C in Fig. 3 is not an acceptable group, and this is so even if A or B actually or potentially interbreeds with C.

A variety of special cases are discussed by de Queiroz et al. (MS in prep.). In each of these cases the resolution of what at first appears to be a major difficulty requires that it be clearly borne in mind that monophyly is the criterion of group membership. A character may be a false indicator of monophyly, and in some cases it is possible to discover this directly. If, for example, A and B in Fig. 3 are females and C is a male, and if these are seen to interbreed and yield offspring with and without character c, then we would conclude that character c is not a character that provides evidence of the

monophyly of C–F. Thus, the cladogram of Fig. 1 would be obtained, and A–C would be an acceptable group. The same reasoning applies if A and B are juveniles and C–F are derived adults; character c would not be considered a synapomorphy of C–F but of A–F instead. In both of these instances direct evidence is obtained (about breeding or ontogeny) that argues against a particular character being a shared homologue inherited from a common ancestor.

Hybridization poses theoretical and practical difficulties for the phylogenetic species concept, but these are not insurmountable. Some problems are avoided by recognizing that although a species (as a lineage of organisms) must have a unique beginning, it need not originate from a single parent species. A species is monophyletic if it includes all and only the descendants of a common ancestor, even if that ancestor was the product of hybridization. The parent species of a hybrid species are, of course, paraphyletic. However, when a cladogram is constructed, positive paraphyly may not be discerned—instead the parent species may appear as unresolved and therefore acceptable groups. Further discussion of hybridization is beyond the scope of the present paper.

Having decided which groups are acceptable under the phylogenetic concept, which of these should be given species rank? This decision must be made because there are monophyletic groups at all levels. Thus, according to our grouping criterion, we could choose to recognize D–F in Fig. 1 as one species and the unresolved group A–C as a second species. But we might choose instead to recognize only one species including organisms A–F—this group is monophyletic and therefore acceptable by our grouping criterion. How shall we decide between such alternatives?

Rosen (1978, 1979) and Nelson and Platnick (1981) proposed that every one of the smallest units that can be identified be given species rank. This suggestion is appealing for several reasons. First, it does away with the problem of infraspecific taxa and categories—there would simply be none! Second, it is probably the case that the smallest discernible units are individuals in the philosophical sense—integrated and cohesive—or that they contain such individuals (i.e., they are “historical entities,” Wiley 1980). In any case actually interbreeding evolutionary individuals are probably no larger than the smallest units, or at least they would not remain so if gene exchange were extensive enough. Third, giving species rank to the smallest recognizable monophyletic or unresolved units pins down the meaning of speciation. Speciation would be the process of origination of a separate lineage characterized by a new trait.

I find this proposal very attractive and urge that it be adopted. However, it would be valuable to distinguish between the two kinds of smallest units, because some questions are appropriately asked only of one kind or the other. Ackery and Vane-Wright (1984; and R. I. Vane-Wright, personal communication) reached a similar conclusion, and suggested that “positively” monophyletic units be called “cladospecies” and that the smallest unresolved units be called “paraspecies.” The term “paraspecies” might perpetuate the failure to distinguish clearly between “positively paraphyletic” groups and unresolved groups, and for this reason de Queiroz et al. (MS in prep.) use “metaspecies” for the smallest unresolved groups. They also suggest that the binomial names of all metaspecies be marked with an asterisk (A–C in Fig. 4) so they can be distinguished at a glance from cladospecies without recourse to the most recent monographic treatment.

Another approach to ranking is possible and may prove desirable in some cases. It might be that recognizing every smallest acceptable group would get quickly out of hand, especially in groups in which asexual reproduction is common. Rather than recognize as a species every distinguishable clone, it might be desirable to employ some other ranking criterion so as to choose more inclusive monophyletic units. Such ranking criteria might include ecological or morphological gaps (perhaps measured in terms of the number of apomorphies). In some cases information about breeding might also enter into the decision. Thus, for example, the observation that organisms from the group D–F in Fig. 1 can interbreed with members of group A–C might lead to the decision that A–F be placed in one species. However, it is very important to recognize that information about interbreeding cannot be used to recognize A–C in Fig. 3 as a species because in this case A–C is an unacceptable group according to the grouping criterion. In other words information about breeding might be used in assigning species rank but can never override the grouping criterion. This is a very different use of breeding information than is made under the biological species concept.

If we chose in some cases not to recognize every smallest acceptable group that is discernible, then ranking criteria would differ from one group of organisms to the next. Thus, although species would be monophyletic or unresolved groups, they might not be comparable in any other attributes. Of course, this is the situation we have now (Davis & Heywood 1963; Raven 1976), except that now we cannot even count on monophyly (Mishler & Donoghue 1982). The phylogenetic concept would simply force us to specify exactly what criteria were used in assigning species rank. Thus, rather than assuming correspondences between morphology, ecology, and

breeding, any such correspondences would have to be detailed in each case.

CONCLUSIONS

I hope to have demonstrated that the biological species concept and biological species definitions perpetuate confusion about (1) the correspondence between breeding groups and morphologically and/or ecologically distinguishable groups, (2) the importance of interbreeding or the lack of it in causing or allowing morphological or ecological divergence, and (3) the distinction between grouping and ranking. As such, I think they stand in the way of a finer resolution of evolutionary patterns and a better understanding of evolutionary processes.

I have argued that for purposes of phylogeny reconstruction, cladistic classification, and the study of evolution, biological species definitions are inappropriate because they can yield non-monophyletic taxa. If our goal is to resolve genealogical relationships as finely as possible—and I, for one, would like to do this—then we need to develop a species concept and definition consistent with this goal. I suggest that the phylogenetic species concept developed by de Queiroz et al., which emphasizes the distinction between grouping and ranking and gives primacy to grouping, is appropriate for this purpose and sidesteps confusions of the past. The phylogenetic definition is practical in application. It can as easily be applied to fossils and asexually reproducing organisms as to extant, sexual ones, and it honestly reflects available evidence without implying correspondences between breeding, morphology, and ecology. More importantly, it yields species that are significant from the standpoint of evolution, that is, monophyletic groups or unresolved groups that may be cohesive individuals. If the phylogenetic species concept were adopted, classifications could, with a minimum number of conventions, accurately and consistently reflect the hierarchy of groups produced by evolution and would therefore be maximally informative about available character information.

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