Individuality, Pluralism, and the Phylogenetic Species Concept

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ABSTRACT: The concept of individuality as applied to species, an important advance in the philosophy of evolutionary biology, is nevertheless in need of refinement. Four important subparts of this concept must be recognized: spatial boundaries, temporal boundaries, integration, and cohesion. Not all species necessarily meet all of these. Two very different types of "pluralism" have been advocated with respect to species, only one of which is satisfactory. An often unrecognized distinction between "grouping" and "ranking" components of any species concept is necessary. A phylogenetic species concept is advocated that uses a (monistic) grouping criterion of monophyly in a cladistic sense, and a (pluralistic) ranking criterion based on those causal processes that are most important in producing and maintaining lineages in a particular case. Such causal processes can include actual interbreeding, selective constraints, and developmental canalization. The widespread use of the "biological species concept" is flawed for two reasons: because of a failure to distinguish grouping from ranking criteria and because of an unwarranted emphasis on the importance of interbreeding as a universal causal factor controlling evolutionary diversification. The potential to interbreed is not in itself a process; it is instead a result of a diversity of processes which result in shared selective environments and common developmental programs. These types of processes act in both sexual and asexual organisms, thus the phylogenetic species concept can reflect an underlying unity that the biological species concept can not.

KEY WORDS: Species concepts, individuality, pluralism, monophyly, cladistics, phylogeny.

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

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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, in press; Hull, 1984, 1987; Kitcher, 1984a, 1984b; Kitts, 1983, 1984; Mayr, 1987; Rieppel, 1986; Ruse, in press; Sober, 1984; Williams, 1985), and to make several points. First, the distinction between individuals and classes is an oversimplification; 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 classes. By "individuals" they meant entities that are "spatiotemporally localized, well-organized, cohesive at any one time, and continuous through time" (Hull, 1987). 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 oversimplified 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, 1984a). 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 subparts. 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," i.e., effects of biological processes, and the latter refer directly to the action of processes. We particularly use species taxa as currently defined for examples 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, in press). 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 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' 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, i.e., 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' 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' 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 spatiotemporally 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 spatiotemporal 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 spatiotemporally 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 programs, 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 spatiotemporal 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 favored agent are impossible. Rather, a number of causal agents are acknowledged to be possible and controversy centers 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 discus-

sion by Holsinger, 1984, in press). 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 interest 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; 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 proven 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 skepticism 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; 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 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. 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

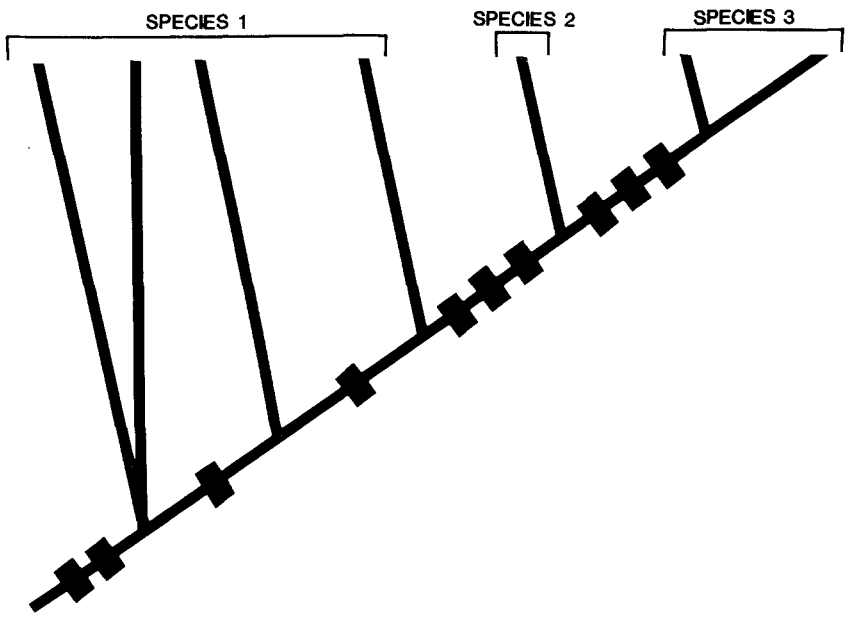

Fig. 1. A hypothetical cladogram showing three named species. Synapomorphies are shown as cross-bars; autapomorphies are not shown. Species 1 is paraphyletic.

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.

An Alternative Concept of Species

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 favored 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 spatiotemporal 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 for example discussion by 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 macroevolu-

tionary 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, paleobiologists, 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 demonstrates how a monistic ranking (and grouping) concept based on interbreeding criteria can obscure actual patterns of diversification. One of us (B. D. M.) 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 — e.g., 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 programs, 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 programs. 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 programs because they share a common ancestor. Reproduction is a relevant process here, but not necessarily sexual reproduction.

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 favor) has

not been applied to the species level. Hennig (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 descendents 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 of "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 descendents 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 spatiotemporal 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 spatiotemporally 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 spatiotemporally 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* spatiotemporally 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 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 (1984a: 314—315). 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. 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. 1) is actually integrated by gene flow, then over time its cladistic structure should approach that of Species 1 in Figure 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. 2) in which a number of unresolved 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. 2) with a 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. 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 2 could acceptably be named a species in a tentative and pragmatic way, pending further study designed to resolve the relation-

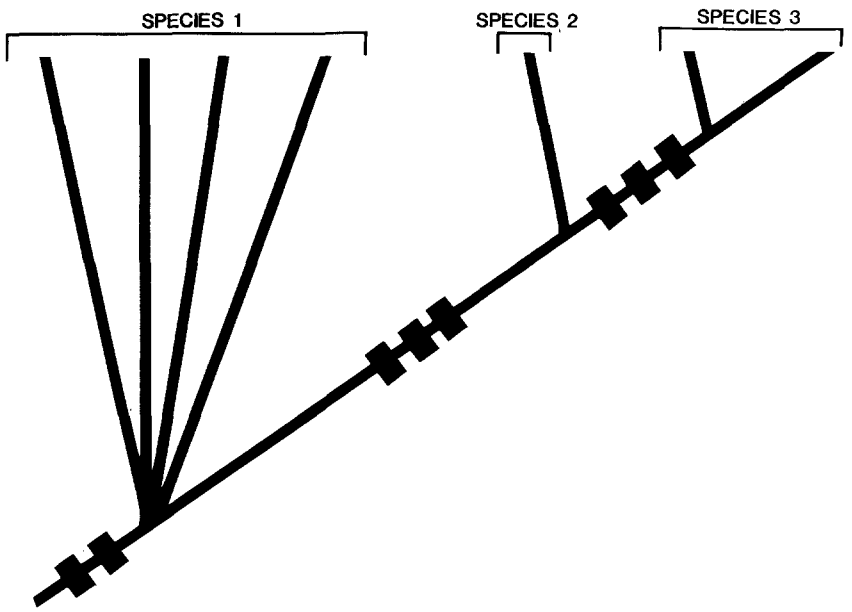

Fig. 2. A hypothetical cladogram showing three named species. Synapomorphies are shown as cross-bars; autapomorphies are not shown. Species 1 is metaphyletic.

ships, 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. 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 paper, this term would clarify similar situations with respect to higher taxa, and may thus prove more widely useful.

CONCLUSION

The "species problem" as discussed in this paper 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 fulfill 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.

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NOTES

[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 lead to some confusion. Second, the operative notion of "individual" comes more from common sense zoology than from logic.

[2] As pointed out by Hull (pers. comm.), 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.

[3] A similar result has been arrived at by Holman (pers. comm.) 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.

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