



Species Concepts: A Case for Pluralism

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SPECIES CONCEPTS: A CASE FOR PLURALISM

We must resist at all costs the tendency to superimpose a false simplicity on the exterior of science to hide incompletely formulated theoretical foundations. (Hull, 1970:37)

It has often been argued that it is empirically true and/or theoretically necessary that “species,” as units in nature, are fundamentally and universally different from taxa at all other levels. Species are supposed to be unique because they are individuals (in the philosophical sense, as opposed to classes)—integrated, co-

hesive units, with a real existence in space and time (Ghiselin, 1974; Hull, 1978). Interbreeding among the members (parts) of a species and reproductive isolation between species are generally believed to account for their individuality. These reproductive criteria are supposed to provide the greater objectivity of the species category and have been suggested as *the* criteria by which species taxa are to be delimited in nature.

Wake (1980) has pointed out that this

conception of species forms the basis upon which Eldredge and Cracraft (1980) have built their formulation of evolutionary process and phylogenetic analysis. In fact, this notion of species seems to underlie much of the recent and growing body of theory which, for convenience, could be called macroevolutionary theory (Eldredge and Gould, 1972; Stanley, 1975; Gould, 1982). Moreover, most recent texts in systematics and ecology are predicated on the idea that species taxa are unique and fundamental (e.g., White, 1978; Ricklefs, 1979; Wiley, 1981). It is therefore important to assess carefully any claim that species do or should possess the properties of individuals, and whether breeding criteria are adequate indicators of individuality.

The "species problem" has yielded an enormous quantity of literature, and it is not the purpose of this paper to provide a review (for which see Mayr, 1957; Wiley, 1978; and papers cited therein). Instead, we will (1) briefly characterize prevailing species concepts, (2) summarize some empirical observations that bear on the species problem, (3) consider the respects in which species taxa as currently delimited by systematists do and do not have the properties of individuals, (4) discuss several choices with which we are faced if all the criteria of individuality are not always met.

We will argue that current species concepts are theoretically oversimplified. Empirical studies show that patterns of discontinuity in ecological, morphological, and genetical variation are generally more complex than are represented by these concepts. Criteria for what constitutes "important" discontinuity appear to vary in response to the vast differences in biology between groups of organisms. In our view, no single and universal level of fundamental evolutionary units exists; in most cases species taxa have no *special* reality in nature. We urge explicit recognition and acceptance of a more pluralistic conception of species, one that recognizes the evident variety and complexity of "species situations." We will

conclude by exploring important consequences of this view for ecology, paleontology, and systematics.

PREVAILING SPECIES CONCEPTS

A consensus appears to have been reached that species are integrated, unique entities. The so-called biological species concept emphasizes that species are reproductive communities within which genes are (or can be) freely exchanged, but between which gene flow does not occur or at least is very rare (e.g., Mayr, 1970). According to this view a species is a group of organisms with a common gene pool that is reproductively isolated from other such groups.

The evolutionary species concept (Simpson, 1961; Grant, 1971; Wiley, 1978, 1981) is an important extension of the concept of biological species, an attempt to broaden the definition to include all sorts of organisms (not just sexually reproductive ones) and to portray the existence of species through time. According to this view species are separate ancestor-descendent lineages with their own evolutionary roles, tendencies, and fates. The ecological species concept of Van Valen (1976) is similar (but see Wiley, 1981), however it emphasizes the "adaptive zone" occupied by a lineage.

Ghiselin (1974) and Hull (1976, 1978) have examined the status of species from a philosophical standpoint. They contend that if species are to play the role required of them in current systematic and evolutionary theory, they must be "individuals" (i.e., integrated and cohesive entities with a restricted spatiotemporal location) rather than "classes" (i.e., spatiotemporally unrestricted sets with defining characteristics). Hull (1980), Wiley (1980, 1981), and Ghiselin (1981) argue that species are fundamentally different from genera, families, and other higher taxa, because they are the most inclusive entities that are "actively evolving."

In general then, species are considered to be the most objectively defined taxonomic and evolutionary units. As Mayr (1970:374) put it, they are "the real units

of evolution, as the temporary incarnation of harmonious, well-integrated gene complexes." They differ from taxa at all other levels, which are considered to be arbitrarily defined and more subjective categories (e.g., Mayr, 1969:91).

For many workers, these views are not only theoretically satisfying but also seem sufficiently unproblematical in application. Many biologists (especially zoologists) seem to be satisfied that, with the exception of some sibling species complexes and rassenkreise, the application of biological/evolutionary species concepts will yield the same sets of organisms that would be recognized as "species" by a competent taxonomist in a museum, or by a person on the street.¹

It must be pointed out, however, that the prevailing species concepts are based on relatively few well-studied groups such as birds and *Drosophila*, groups in which discontinuities in the ability to interbreed are relatively complete, and discontinuities in morphological and ecological variation coincide well with the inability to breed in nature. It also must be pointed out that even though relatively few groups have been studied in detail, a correspondence between morpho-

logical, ecological, and breeding discontinuities is often simply assumed.

The acceptance of biological/evolutionary species concepts has not been universal. In particular, the botanical community has not wholeheartedly taken them up, and alternatives have been proliferated.² It seems clear that the group of organisms on which one specializes strongly influences the view of "species"

² Initially, the biological species concept was embraced and promulgated by plant systematists interested in evolution (Stebbins, 1950; Grant, 1957). Cronquist (1978) detailed Grant's efforts (from 1956 to 1966) to apply the biological species concept in *Gilia* (Polemoniaceae). It very soon became apparent that the biological species concept was fraught with difficulties, but Grant chose to amend the concept (rather than abandon it altogether), first (1957) with the notion of the syngameon (i.e., the unit of interbreeding higher than the species), later (1971) by adopting an evolutionary species concept. Finally, in the second edition of his classic book on plant speciation, Grant (1981) treats species in a more flexible and pluralistic manner. Some botanists (e.g., Stebbins, 1979:25) continue to feel that the biological species concept, or some modification of it, is the only suitable framework for understanding plant diversity. However, many (perhaps most) botanical systematists remain rather skeptical about the general applicability of the concept in botany (Davis and Heywood, 1963; Raven, 1976; Cronquist, 1978; Levin, 1979; Stevens, 1980a).

¹ Gould (1979) and others have defended the biological species concept on the grounds that the same taxa recognized by western taxonomists are recognized by tribespeople in New Guinea, etc. There are several problems with this kind of argument. First, it is not clear that this finding constitutes an independent test because, after all, New Guinea tribespeople are human too, with similar cognitive principles and limitations of language. It should also be borne in mind that the observer is by no means neutral. Folk taxonomies have been collected by people with a knowledge of evolution and modern systematic concepts. Second, it is generally not a strong argument to show that a pre-scientific society has recognized something that modern science currently accepts. Surely a modern astronomer would not consider it very strong evidence that a primitive mythology supported one cosmological theory over another. Finally, the taxa recognized by western taxonomists (and often by natives at some level of their linguistic hierarchy) in these instances are not known to be biological species—for the most part they are morphological units that are *believed* to be reproductively isolated from other such units.

The different attitudes of zoologists and botanists towards the concept of species may be of interest to historians, sociologists, and philosophers of science. For organismic and evolutionary biology the "modern synthesis" of the 1930's and 1940's may have represented a revolution in the sense of Kuhn (1970). For systematists, the principal outcome was the biological species concept. Zoologists (especially vertebrate systematists) appear to have largely accepted the new paradigm and to have entered a period of "normal science," applying the concept in particular cases ("puzzle solving"). While problems like sibling species, semispecies, and subspecies have become apparent, these have generally not prompted a critical evaluation of the paradigm or a proliferation of alternatives. In contrast, in the botanical community the biological species concept was soon found to be inapplicable or of difficult application and likely to lead to confusion. This resulted in a groping for alternatives and a defense of older concepts. In this regard, the historical development of species concepts in botany seems to fit better Feyerabend's (1970) characterization of scientific change as the simultaneous practice of normal science and the proliferation of alternative theories.

that one develops. It also seems clear that in order to fully appreciate biological diversity (for purposes of developing general concepts), it is essential to study a variety of different kinds of organisms, or at least take seriously those who have.³

Numerous attacks have been leveled at the biological/evolutionary species concepts. Many of these have been concerned primarily with whether they are operational (e.g., Sokal and Crovello, 1970). However, as Hull (1968, 1970) has pointed out, a concept cannot be completely operational and still be useful for the growth of science. The critical question is whether a concept is operational *enough* to be useful as a conceptual framework. Considerations of operability, while certainly of interest, are not central to the argument developed below, which primarily concerns the theoretical adequacy of prevailing species concepts.

EMPIRICAL CONSIDERATIONS

In our view, a theoretically satisfactory species concept must bear some specifiable relationship to observed patterns of variation among organisms. It is *not* acceptable to adopt a definition of species simply because it conveniently fits into some more inclusive theory, e.g., a theory

of evolutionary process. A species concept is, in effect, a low level hypothesis about the nature of that variation, itself subject to empirical tests. Therefore, in this section, we summarize some relevant empirical findings, many of which have not been generally recognized.

The Noncorrespondence of Discontinuities

The reason for discontent among botanists and other workers is not that they have been unable to perceive discontinuities in nature. Instead, it has become apparent that there are many kinds of discontinuities, all of which may be of interest (Davis and Heywood, 1963:91). The question is, how well do various discontinuities correspond; i.e., are the same sets of organisms delimited by discontinuities when we look at morphology, as when we look at ecology, or breeding? The answer appears to be that there is no necessary correspondence. Stebbins (1950), Grant (1957, 1971, 1981), Stace (1978) and many others have discussed hybridization, apomixis, polyploidy, and anomalous breeding systems in plants and have clearly documented the frequent noncorrespondence of different kinds of discontinuities. In some groups there is complete reproductive isolation between populations that would be recognized as one species on morphological grounds (i.e., "sibling species," as in some groups of *Gilia* (Grant, 1964), and *Clarkia* (Small, 1971)), and in many other groups of plants the interbreeding unit encompasses two to many morphological units (e.g., *Quercus* (Burger, 1975)).

It has also become clear that discontinuities in morphological variation or in the ability to interbreed do not necessarily correspond to differences in ecology ("niche"?). The early work of Turesson (1922a, b) in Europe, and of Clausen, Keck, and Hiesey (1939, 1940) in North America, demonstrated that ecotypes "may or may not possess well-marked morphological differences which enable them to be recognized in the field" (Stebbins, 1950:49). The great extent to which

³ The zoologists initially responsible for developing the biological species concept were aware of the difficulties in applying the concept in some groups of animals and many groups of plants. Dobzhansky (1937, 1972) consistently pointed out the diversity of "species situations" observable in nature. Mayr (1942:122) was careful to point out differences between plants and animals, and difficulties in the practical application of the biological species concept in some cases. Particularly rigid versions of the biological species concept have been promulgated more recently, in attempted generalizations that have shown a startling lack of concern for the biology of the majority of organisms on earth. Mayr (1982) has examined the resistance of botanists to the biological species concept and concluded that "the concept does not describe an exceptional situation" (p. 280). But he grants some justification to the ideas of "certain botanists" who question "whether the wide spectrum of breeding systems that can be found in plants can all be subsumed under the single concept (and term) 'species'" (p. 278).

local populations of the same biological or morphological species are physiologically differentiated and adapted to their particular environments is only now being realized (Mooney and Billings, 1961; Antonovics et al., 1971; Antonovics, 1972; Bradshaw, 1972; Kiang, 1982).

If noncorrespondence is prevalent, then strict biological species will not necessarily have anything in common but reproductive isolation. It might be argued that a species concept that unambiguously reflects one aspect of variation may be preferable to one that ambiguously reflects several things. But why should we necessarily pin species names on sets of organisms delimited by reproductive barriers? Why not choose, for example, to name morphological units instead?

One argument for pinning species names on reproductively isolated groups is that breeding discontinuities are thought to be more clear-cut than morphological ones and therefore less arbitrary. However, Ornduff (1969) has summarized the complexity of the reproductive biology of flowering plants and pointed out the difficulty of applying rigid species delimitations based on interfertility. When variation in the ability to interbreed is examined in detail, we find discontinuities of many different degrees and kinds. Groups of organisms range from completely interfertile to completely reproductively isolated. Hierarchies or networks of breeding groups vary in complex ways in space and time. Therefore, even if we were to decide that breeding discontinuities were theoretically the most important kind of discontinuity, and the ones that species names should reflect, the choice of what constitutes a significant discontinuity remains problematical.

A second argument for the importance of reproductive barriers is that gene flow prevents significant divergence while a lack of gene flow allows it. However, this now appears not to be the case. If a population is subjected to disruptive selection, there can be divergence even in the face of gene flow (Jain and Bradshaw,

1966). In these instances it appears that some means of reproductive isolation will usually evolve, but such isolation follows initial divergence. Moreover, allopatric populations can remain morphologically similar for very long periods or they can diverge morphologically (see discussion of this point by Bremer and Wanntorp, 1979a). This morphological divergence may or may not be accompanied by reproductive isolation, though it appears likely that eventually a reproductive barrier will result. The point is that morphological divergence and the attainment of means of reproductive isolation can be uncoupled events in time and space. Levin (1978:288–289) concluded:

If we adhere to the biological species concept—the integrated reproductive communities—described by Mayr, then speciation is capricious . . . Isolating mechanisms are not the cause of divergent evolution, nor are they essential for it to occur.

A related, larger-scale argument for the importance of reproductive barriers is that groups that are reproductively isolated for long periods of time are at least evolutionarily independent (whether or not they diverge morphologically), making them effectively separate entities. Reproductive barriers indeed may often be important in this way, but other factors such as ecological role and homeostatic “inertia” are important as well. Because of the complex nature of variation in each of these factors, and because different factors may be “most important” in the evolution of different groups, a *universal* criterion for delimiting fundamental, cohesive evolutionary entities does not exist.

Questionable Internal Genetic Cohesion

The notion of integration and internal cohesion is central to biological/evolutionary/individualistic species concepts. In this paper we will follow the common assumption that “cohesion” means genetic cohesion maintained via gene flow, a notion that has recently been explicitly formulated (Wiley and Brooks, 1982). However, Hull (1978) has pointed out that

other factors such as internal homeostasis and "external environment in the form of unitary selection pressures" (p. 344) may contribute to or confer cohesion. It seems to us likely that "cohesion," and the factors responsible for it, will differ from one group of organisms to another and from one level in the hierarchy to another.

Ehrlich and Raven (1969) pointed out that the extent of gene flow seems to be very limited in many organisms and may not account for the apparent integrity of the morphological units we recognize in nature. Bradshaw (1972:42) suggested that "effective population size in plants is to be measured in meters and not in kilometers." Endler (1973) studied clinal variation and concluded that "gene flow may be unimportant in the differentiation of populations along environmental gradients" (p. 249). Levin and Kerster (1974) thoroughly reviewed and analyzed the literature concerning gene flow in seed plants and concluded that "the numbers [of individuals] within panmictic units are to be measured in tens and not hundreds" (p. 203). These same points were reiterated by Sokal (1973), Raven (1976), and Levin (1978, 1981). Levin (1979:383) stated:

The idea that plant species are Mendelian populations wedded by the bonds of mating is most difficult to justify given our knowledge about gene flow. Indeed a contrary viewpoint is supported. Populations separated by several kilometers may rarely, if ever, exchange genes and as such may evolve independently in the absence of strong or even weak selective differentials.

Lande (1980) has stressed that there has been an overemphasis on the genetic cohesion of widespread species and argued that "of the major forces conserving phenotypic uniformity in time and space, stabilizing selection is by far the most powerful" (p. 467). Grant (1980:167) suggested that "the homogeneity of species is due more to descent from a common ancestor than to gene exchange across significant parts of the species area."

Jackson and Pound (1979) critically reviewed much of this literature and rightly pointed out that there is little rigorous

evidence in animals to support or to reject the generality of any statement about gene flow because detailed studies are rare. They concluded, however, that data "seem sufficient to indicate that gene flow in plants can be limited due to local or leptokurtic dispersal of pollen and seeds" (p. 78). It is important to keep in mind that population genetic theory predicts that a small amount of migration between populations may be sufficient to maintain genetic similarity in the absence of differential selection (Lewontin, 1974:212-216). Clearly, determining the relative importance of factors such as gene flow, developmental homeostasis, and selection in nature will require rigorous population genetic theory (e.g., Lande, 1980) and careful quantification of empirical data, rather than qualitative, anecdotal arguments.

Evolutionary biologists are just beginning to understand gene flow in plants and animals, but have hardly begun to address the complicated patterns of gene exchange present in the fungi, bacteria, and "protists." A kind of chauvinism has so far restricted discussions of gene flow to comparisons of biparental sexual organisms and asexual ones. Complex patterns of sexuality are present in the fungi (Cléménçon, 1977); intricate incompatibility systems, as well as incompletely understood parasexuality cycles, make the simplistic application of the biological species concept impossible in most cases. The existence of discrete, integrated genetic lineages is even less likely in the "Monera" (Cowan, 1962). There probably are very few absolute barriers to genetic exchange in bacteria, because of the phenomena of DNA-mediated transformation, phage-mediated transduction, and bacterial conjugation (Bodmer, 1970).

ARE SPECIES TAXA INDIVIDUALS?

In our view, the empirical considerations discussed above indicate that in many (perhaps most) major groups of organisms, actual patterns of variation are such that the species taxa *currently recognized* by taxonomists cannot be consid-

ered discrete, primary, and comparable "individuals," integrated and cohesive via the exchange of genes, fundamentally different from taxa at other levels. Variation in morphology, ecology, and breeding is enormous and complex; there are discontinuities of varying degree in each of these factors and the discontinuities are often not congruent. There may often be roughly continuous reduction in the degree of cohesion due to gene flow as more inclusive groups of organisms are considered. The acquisition of reproductive isolating mechanisms appears in many cases to be fortuitous and such isolation is neither the cause of morphological or ecological divergence nor is it necessary for divergence to occur.

Although many currently recognized species do not meet one important criterion of "individuality," namely cohesion and integration of parts, another important criterion often is met, namely restricted spatiotemporal location (i.e., units united by common descent). These units are not strictly "individuals" or "classes," but clearly they can function in evolutionary theory and phylogeny construction. Wiley (1980) called such units "historical entities," but applied this term only to taxa above the species level.

We should mention, as a disclaimer, that although many species taxa (as currently delimited) cannot be considered unique, individualistic units, this does not mean that all species taxa are not. In some groups of organisms, biological species may conform in all respects to the philosophical concept of individual. We simply suggest that this condition is a "special case," and that unwarranted extrapolations have been made from a very few groups of organisms to organisms generally.

SOME OPTIONS

As discussed above, in many plant and some animal groups, evolutionary processes (i.e., replication and interaction in the sense of Hull, 1980) occur primarily on a small scale (even when extrapolated over many generations) relative to the

traditional species level. In such groups, the units in nature that are more like individuals are actually interbreeding local populations, and therefore, the basal taxonomic unit (the species) is currently more inclusive than the basal evolutionary units (the populations). This means that many presently recognized species taxa are, at best, historical entities. If this is the case, and if we want species taxa that are more fully individuals, can we bring taxonomic practices in line with our theoretical desires, and at what cost? If we cannot, or if the costs are too great, are there any theoretically acceptable alternatives, and what would they entail?

We formulate here three options with which we are faced and reject the first two. In the next section we explore some implications of the third alternative.

(1) Alter the usage of "species" to equal "evolutionary unit," i.e., attempt to locate all of the effectively isolated and independently evolving populations and apply species names to them.

(2) Alter the usage of "species" to equal the "cenospecies" or "comparium" (see Stebbins, 1950; Grant, 1971), i.e., recognize as the basic taxonomic units only those taxa that are *completely* intersterile.

(3) Apply species names at about the same level as we have in the past, and decouple the basal taxonomic unit from notions of "basic" evolutionary units.

We reject choice (1) for several reasons, some practical and some theoretical. In a practical sense, formally naming whatever the truly genetically integrated units turned out to be would be disastrous. There are certainly very many such units, they are at best very difficult to perceive even with the most sophisticated techniques and in the most studied organisms, and these units are continuously changing in size and membership from one generation to the next. At any one time we can never know which units will diverge forever.

Rosen (1978, 1979) has discussed and adopted a species concept quite similar to choice (1). While we would generally

agree with him that populations with apomorphous character states are units of evolutionary significance (1978:176), we could not agree that species should be "the smallest natural aggregation of individuals with a specifiable geographic integrity that can be defined by any current set of analytical techniques" (1979:277). Since we could probably distinguish each individual organism, or very small groups of organisms, on the basis of apomorphies (if we looked hard enough), why shouldn't each of these units be given a Linnaean binomial?

There is a more important, theoretical reason for rejecting alternative (1), one that we have alluded to above. A pervasive confusion runs through much discussion of species: the erroneous notion that a single basal evolutionary unit is somewhere to be found among all the possible units that could be recognized. There are *many* evolutionary, genealogical units within a given lineage (Hull, 1980)—a rough hierarchy or network of units, which may be temporally and spatially overlapping. Thus, in the search to find *the* evolutionary unit, one is on a very "slippery slope" indeed. Units all along this slope may be of interest to evolutionists, depending on the level of focus of the particular investigator. These units do require some sort of designation in order to be studied, but a formal, hierarchical Linnaean name is not necessary.

Option (2), in many instances, would represent the opposite extreme (an attempt to locate the "top" of the slippery slope). Absolute reproductive isolation would be used as the overriding ranking criterion. If two organisms could potentially exchange genes, either directly or through intermediates, they would be placed in the same species taxon. There are several reasons why we reject this alternative.

First, it is unclear that reproductive criteria necessarily provide species taxa that are useful for purposes of phylogeny reconstruction and historical biogeography. As Rosen (1978, 1979) and Bremer and Wanntorp (1979a) have pointed out, "bi-

ological species" may be paraphyletic assemblages of populations united only by a plesiomorphy, i.e., all those organisms that have not acquired a means of reproductive isolation. If reproductive criteria are to be useful for cladistic analysis, it is necessary to determine which modes of isolation arose as evolutionary novelties in a group.

Our second objection to option (2) has to do with the problem of measuring "potentiality." There have been numerous comments on the inadequacy of potential interbreeding as a ranking criterion, and even strong proponents of the biological species concept have rejected potential interbreeding as a part of their species definitions. Under certain conditions, very disparate organisms can be made to cross. If we adopted this option, the family Orchidaceae, with approximately 20,000 species at present (covering a great range of variation), might be lumped into just a few species because horticulturalists have produced so many bi- and pluri-generic hybrids. The universal application of any one criterion will undoubtedly obscure important patterns of variation in other parameters.

SPECIES LIKE GENERA

If we adopted alternative (3), what would happen to the species category? Would species taxa necessarily be theoretically meaningless entities? Are all alternatives to biological/evolutionary/individual species concepts devoid of theoretical interest as implied by Eldredge and Cracraft (1980:94)?

We would agree that if species were simply phenetically similar groups of populations they might indeed be unsatisfactory for many purposes. The application of species concepts like those of Cronquist (1978) and of Nelson and Platnick (1981) may yield species taxa that are not useful from the standpoint of re-

⁴ The species concepts of Cronquist and of Nelson and Platnick are as follows:

Cronquist (1978:15): "... the smallest groups that

constructing phylogenies (see discussion by Beatty, 1982).⁴

However, we think that one form of option (3) may provide theoretically meaningful units. In groups where the actually interbreeding units are small relative to the morphologically delimited units, species can be considered to be like genera or families or higher taxa at all levels. That is, they are assemblages of populations united by descent just as genera are assemblages of species united by descent, etc. If we required that species be monophyletic assemblages of populations (to the extent that this could be hypothesized), then they could play a role in evolutionary and phylogenetic theory just as monophyletic taxa at all levels can. Theoretical significance does not reside solely in the basal taxonomic units or in units that are "fully individuals."

If we recognize that species are like genera, and insist that they be monophyletic, then we are faced with the problems of assessing monophyly and of ranking, problems that plague systematists working at all levels. Several different concepts of monophyly have been employed by systematists, but none of them explicitly at the species level (see discussion by Holmes, 1980). We favor Hennig's (1966) concept of monophyly (except explicitly applied at the species level) but are fully aware of the difficulties in its application at low taxonomic levels (Arnold, 1981; Hill and Crane, 1982). In particular, the difficulty posed by reticulation (hybridization) (Bremer and Wanntorp, 1979b) may be especially acute at lower taxonomic levels. Using synapomorphy as evidence of monophyly requires that the polarity of character states be determined, and again this may be an especially difficult problem near the species level. Polarity assessments will be possible to a greater or lesser extent

depending on the certainty with which out-groups are known (Stevens, 1980b).

As noted previously, in order to use reproductive isolation as evidence of monophyly, it would be necessary to determine which means of reproductive isolation are apomorphies at a given level, and which are not. An example of the difficulty of applying a Hennigian concept of monophyly is the very real possibility of "paraphyletic speciation." If speciation by peripheral isolation happens frequently, then a population (geographically defined), which has developed some apomorphic feature (such as a morphological novelty or an isolating mechanism) with respect to its "parent" species, may often be cladistically more closely related to some part of the parent species than to the remainder (see discussion and example in Bremer and Wanntorp, 1979a). In such a case, we would take the (perhaps controversial) position that if the population is to be recognized as a formal species taxon, and if the phylogenetic relationships of the populations in the parent species can be resolved, then the taxonomist should not formally name the parent "species" (which has now been found to be a paraphyletic group), but instead name monophyletic groups discerned within it. Conversely, however, if cladistic structure within the parent species cannot be resolved, then in our view it would be acceptable to provisionally name it as a species (even if the populations included within shared no apomorphy).

This example illustrates the fact that even when monophyletic groups are delimited, the problem of ranking remains since monophyletic groups can be found at many levels within a clade. Species ranking criteria could include group size, gap size, geological age, ecological or geographical criteria, degree of intersterility, tradition, and possibly others. The general problem of ranking is presently unresolved, and we suspect that an absolute and universally applicable criterion may never be found and that, in-

are consistently and persistently distinct, and distinguishable by ordinary means."

Nelson and Platnick (1981:12): "... the smallest detected samples of self-perpetuating organisms that have unique sets of characters."

stead, "answers" will have to be developed on a group by group basis.

SOME CONSEQUENCES OF PLURALISM

We have outlined a concept of species (i.e., "species like genera") that may be appropriate for groups of organisms in which certain conditions obtain. However, we think that a variety of species concepts are necessary to adequately capture the complexity of variation patterns in nature. To subsume this variation under the rubric of any one concept leads to confusion and tends to obscure important evolutionary questions. As Hull (1970; see epigraph) has argued, we must resist the urge to superimpose false simplicity. If "species situations" are diverse, then a variety of concepts may be necessary and desirable to reflect this complexity.

Many theories in biology appear to lack the universality of theories in other natural sciences. Often the problem is to decide which one of several theories (not necessarily mutually exclusive) applies to a particular situation (for a specific application of this theoretical pluralism to evolutionary biology, see Gould and Lewontin, 1979). A satisfactory general theory is one in which the number of subtheories is kept to a minimum, but not reduced to the point where important patterns and processes are obscured. The evaluation of how well a theoretical system "accounts for" patterns in the world is problematical, and we cannot offer any generally applicable criterion for making such an evaluation. However, in the case of species, we think that the search for a universal species concept, wherein the basal unit in evolutionary biology and in taxonomy is the same, is misguided. In

our opinion, it is time for "species" to suffer a fate similar to that of the classical concept of "gene."⁵

We should recognize that species taxa have never been, and very probably cannot be made readily comparable units. This observation has a number of important theoretical implications. Ecologists must consider the extent to which "species" can be considered equivalent and comparable from one group of organisms to another. Population sizes and structures, gene flow, social organization, the nature of selective factors, and developmental constraints differ in multifarious ways. This means that it is imperative that systematists be explicit about the nature of variation in, and the properties of, the species that they recognize in the groups they study. In turn, the users of species names must at all times be aware that "species are only equivalent by designation, and not by virtue of the nature or extent of their evolutionary differentiation" (Davis and Heywood, 1963: 92). As obfuscatory as this may seem, comparative biologists must not make inferences from a species name without consulting the systematic literature to see what patterns of variation the name purports to represent.

These considerations are also important to paleontologists, who make inferences about, and from, "fossil species," and imply correspondences between variation in morphology, ecology, and breeding. It is perplexing that some quite innovative paleontologists, such as Eldredge and Gould, have uncritically retained the biological species concept in their work. As we have shown, there are many reasons why species should not be treated as particles or quanta. Paleontologists should consider exactly what macroevolutionary theories require species to be. For many purposes they may not require species that are completely individuals, but simply monophyletic lineages. If units that are cohesive via gene flow are an absolute requirement, then fossils may not provide appropriate evidence.

Finally, what are the implications for

⁵ Initially the "gene" was considered to be *the* unit of heredity, but the classical concept of gene has been replaced by several concepts which stand in a complex relation to one another (Hull, 1965). The use of a disjunctive definition (Hull, 1965) allows a single term to designate a complex of concepts. However, this can become so confusing that it may be desirable to replace (at least in part) an old terminology with a new set of terms with more precise meanings.

the systematist of a pluralistic outlook on species? Systematists working on relatively little known organisms should not assume that concepts derived from other groups of organisms are necessarily applicable. Instead, in each group the systematist is obligated to study patterns of variation in morphology, ecology, and breeding, and to detail the nature of the correspondences among these patterns. It is essential that the ways in which names are applied to taxa at all levels be stated explicitly.

If we adopt a case by case approach and urge specialists to unabashedly develop concepts for their particular groups, are we saying that "anything goes"? Of course, the answer is no. We are only suggesting pluralism within limits. Taxa (including species) recognized by systematists must have a specifiable relationship to theoretically important variation, more specifically, we have argued that species taxa should be phylogenetically meaningful units. There may not be a *universal* criterion to arbitrate between conflicting species classifications of a given genus, but through the complex process that is science, the community of involved workers can and will hammer out criteria for making such decisions.

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NONEQUILIBRIUM EVOLUTION AND ONTOGENY

The theory of nonequilibrium evolution (Wiley and Brooks, 1982) presents evolutionary biologists with quite a challenge. Some must decide whether it threatens their research programs. Others, those who have criticized neo-Darwinism in the past, must decide whether it offers a better alternative in the study of organismic order and change. In either case, this new idea must be accepted as explaining biological evolution better than current theories (i.e., better corroborated), or rejected because of internal inconsistencies, untestability, or falsified predictions. Denying or ignoring it will have no effect on its veracity.

The basis of the theory appears to be that species are always dissipative systems, continually ascending the information entropy curve because of intrinsically generated complexity. A corollary of this would be that a descendent species will never be less informationally complex than its ancestral species at the latter's least complex point. Brooks and Wiley account for this in two ways. First, they note that

Those information systems which survive a speciation event will occupy a lower entropy state than the ancestor at its most complex, but all such survivors plus the epiphenotypes not surviving invariably sum to a higher entropy level than the ancestor, even at its most complex. (Wiley and Brooks, 1982:16)

Although I accept this statement's validity, it is not empirically useful, because one would have to know the information levels of all parts of a descendent species, including those that were eliminated at speciation. Another prediction is bolder.

Any change in the information of a species must result in increased complexity, and a higher entropy state, at least initially. (Wiley and Brooks, 1982:12)

or, $S_p \leq S_a < S_{a+p}$

Where S_p is the entropy state of the ancestral canalized information system (the plesiomorphic species), S_a is the entropy state of the descendent (apomorphic) species, and S_{a+p} is the entropy state of the ancestral system at its most complex—immediately before speciation (Wiley and Brooks, 1982:7).