

THE EVOLUTIONARY SPECIES CONCEPT RECONSIDERED

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Abstract

Wiley, E. O. (Division of Fishes, Museum of Natural History, University of Kansas, Lawrence, KS 66045). 1978. *Syst. Zool.* 27:17-26.—The concept of species (as taxa) adopted by an investigator will influence his perception of the processes by which species originate. The concept adopted should have as universal applicability as current knowledge permits. Simpson's definition of a species is modified to state: *a species is a lineage of ancestral descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.* This definition is defended as that which has widest applicability given current knowledge of evolutionary processes. Four corollaries are deduced and discussed relative to other species concepts: (1) all organisms, past and present, belong to some evolutionary species; (2) reproductive isolation must be effective enough to permit maintenance of identity from other contemporary lineages; (3) morphological distinctiveness is not necessary; and (4) no presumed (hypothesized) single lineage may be subdivided into a series of ancestral-descendant "species." The application of the evolutionary species concept to allopatric demes and to asexual species is discussed and it is concluded that the lack of evolutionary divergence forms the basis for grouping such populations into single species. It is suggested that some ecological species definitions lead to under-estimations of the rate of extinction due to interspecific competition because their logical framework excludes unsuccessful species from being species. Finally, the implications of accepting an evolutionary species concept to the field of phylogeny reconstruction are discussed. [Species concepts; evolution; phylogeny reconstruction.]

In all probability more paper has been consumed on the questions of the nature and definition of the species than any other subject in evolutionary and systematic biology. In my opinion this is because the species is usually viewed as an essential entity in the evolutionary process. A species, in the phylogenetic sense, may be viewed as the largest aggregate of individual organisms that evolve as a unit. There has been much investigation of the process, but the questions of what a species is and how species originate are far from solution. Sokal (1973) has suggested that there are two major problems, an adequate species definition, and the origin of species. I agree, but the two problems are not separate. The definition of the word species will be built on a species concept and the concept itself will profoundly affect the way in which investigators view the origin of the species they study. As Popper (1968), Eldredge and Gould (1972), and others have pointed out, the concepts and theories an investigator holds influence how

that investigator views the "facts" of nature. This is as true for the species concept as it is for the concepts of relativity theory and quantum mechanics. I submit that the conceptual problems of species definitions are no worse than the conceptual problems of many other words in science.

The extensive literature regarding the histories of various species concepts has been reviewed by Mayr (1957, 1963, 1969), Simpson (1961), Dobzhansky (1970), Grant (1971), Sokal (1973), and Sneath and Sokal (1973), among others. An anthology of papers on species concepts has been compiled by Slobodchikoff (1976; see Platnick, 1977, for significant omissions). Another historical review is unwarranted and I refer the interested reader to these works and references therein. Instead, I will attempt to resurrect and defend the species concept of Simpson (1961; see also Ghiselin, 1969; Grant, 1971) as best suited for dealing with the species and its origins.

Any species concept "adopted" in light

of current knowledge must, in my opinion, fulfill several roles. (1) It must have as universal validity as current knowledge permits. This would be reflected in its applicability to species through time, to asexual as well as sexual species, to plants as well as to animals. (2) It should make possible the formulation of an hypothesis that a particular group of organisms either comprises a species or does not. The hypothesis must be testable in principle (cf. Hempel, 1965). (3) It must subsume within its logical framework all valid special case definitions of species. (4) It must be capable of dealing with species as spatial, temporal, genetic, epigenetic, ecological, physiological, phenetic, and behavioral entities. (5) It must clearly specify what types of species origins are possible and what types are not possible. This final role is essential to the testability in principle of the concept itself, for if the concept permits everything and prohibits nothing, it is scientifically useless (Popper, 1968).

OPERATIONALISM AND SPECIES CONCEPTS

Some biologists (for example, Ehrlich, 1961; Sneath and Sokal, 1973) have argued that a species definition must be "operational" within the context of the philosophical school of Operationalism espoused by Bridgmann (1945) among others. Operationalism has no doubt been beneficial in influencing scientists to clarify their concepts and definitions. However, Hull (1968) has argued that pure Operationalism is not possible in science and that species concepts and definitions do not have to conform to operationalist philosophy to be scientific (see also Hempel, 1966). In my opinion, Operationalism has been found wanting because its "operational" definitions were either circular (Popper, 1968) or failed to fulfill their set goal of separating, by definition, the cognitively meaningful from the cognitively meaningless. If "operational" definitions within an operationalist philosophy are flawed in these ways, then there can be little justification

for criticizing various species definitions because they are not "operational." Furthermore, there can be little justification for applying pure Operationalism to either systematic or evolutionary philosophy. It should be recognized that the critics of "non-operational" species concepts (cf. Sokal and Crovello, 1970; Sneath and Sokal, 1973) have themselves been unable to supply an "operational" definition. Perhaps this is because the word "species" is a universal, and universals cannot be defined in an operational manner (Popper, 1968).

DEFINITION OF THE EVOLUTIONARY SPECIES CONCEPT

I propose that a simple modification of Simpson's (1961:153) species definition fulfills the criteria discussed above. A *species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.*¹ This definition implies that (1) species can be thought of as individuals rather than classes (cf. Ghiselin, 1966, 1974; see discussion by Hull, 1976, and comment by Mayr, 1976), and (2) that species are historical, temporal, and spatial entities. The definition is empirical in that it permits hypotheses to be derived from it

¹ Simpson's definition states: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." Both definitions stress unity (as does Ghiselin's, 1974) and both imply that the species is the most inclusive unit of evolution. My definition has the advantage of not implying that species must change (evolve). If species go through a rapid (or even saltatory) phase of evolutionary change and then settle down to a longer period of relative stasis (cf. Eldredge and Gould, 1972), then "evolving" is not to be preferred over "maintaining identity" as species may maintain their identity relative to other species with or without changing. "Identity" as used here connotes individual identity and does not connote either stasis or change in morphology. As an analogy: I have maintained my own identity through the years in spite of the fact that my morphology has changed substantially from age 6 to present (also see Vendler, 1975, for other discussions of individuality).

which can be tested in fact or principle (i.e., the concept of empiricism advocated by Hempel, 1965). For example, we may frame the hypothesis, "these two populations (or groups of populations) maintain separate identifiable evolutionary lineages." Evidence used to test such an hypothesis can come from a variety of sources depending on the nature of the organism and the genetic, phenetic, spatial, temporal, ecological, biochemical, and/or behavioral evidence which is available to test the question. Whether a group of organisms is or is not a species then becomes an hypothesis to be tested.

LOGICAL COROLLARIES OF THE DEFINITION

Logical corollaries are those statements or implications which follow directly from an axiom, a definition, or an hypothesis. The evolutionary species concept has several logical corollaries which permit its evaluation. I do not suggest that the corollaries outlined below are the only corollaries possible.

Corollary 1.—All organisms, past and present, belong to some evolutionary species. This corollary is logically evident from the observation that every organism belongs to a lineage including at least its parents (Vendler, 1975). To deny this, one would have to invoke spontaneous generation. Evolutionary species differ from supraspecific taxa in that evolutionary species are lineages or continua whereas higher taxa are groups of separate lineages linked by past continua. Thus, higher taxa are historical constructs whose sole basis for existence is dependent on how accurately they document past continua whereas evolutionary species are the extinct or living continua themselves. In other words, evolutionary species make history, natural higher taxa (monophyletic groups) are history, and un-natural higher taxa (para- and polyphyletic groups) misrepresent history.

In terms of classification, as opposed to pattern and process, all organisms belong to a species, but not all species necessarily belong to a higher taxon such as a fam-

ily or order (I exclude from this discussion the category genus because our system of nomenclature demands that every species belong to a genus). As Goldschmidt (1940), Schindewolf (1950), Løvtrup (1974) and others have asserted, phylogenetic evolution has proceeded from the apex to the base. Therefore, natural phylogenetic classification must also proceed from the apex to the base if it is to reflect the pattern of evolution.

No genus could have originated before the family in which it belongs originated. By this I do not mean that genera, families, or any other supraspecific taxa evolve. What I mean is that the stem species of a genus cannot originate before the stem species of the family to which that genus is a member. This is a logical corollary of the axiom of continuity of descent and simply a rejection of spontaneous generation. It is logically derived from the assertion that higher taxa originate concurrently with their stem species, i.e., that the family at the time of its origin was composed of a single evolutionary species (Hennig, 1966; Wiley, 1977; for another point of view see Platnick, 1976, 1977). For example, the ancestral species of the gar family *Lepisosteidae* must have originated before either of the ancestral species of this family's included genera, *Lepisosteus* and *Atractosteus*. On the practical level of reconstructing phylogenies, the synapomorphies of the family *Lepisosteidae* are hypothesized to have originated before the synapomorphies of the genus *Lepisosteus*. On the theoretical level, when I make such a statement I mean that the characters which I hypothesize as synapomorphic for *Lepisosteidae* are those characters which are hypothesized to have arisen in the stem species of the family as autapomorphies and passed on to the descendants of that species (the ancestral stem species of *Lepisosteus* and *Atractosteus*). And, the stem species of these genera later developed their own sets of separate autapomorphies which were passed on modified or unmodified to their descendants. I do not wish to im-

ply that any particular set of characters are "family characters" or that another set are "generic characters." The synapomorphies which characterize the stem species of Lepisosteidae do not make this taxon a family, the significance of Lepisosteidae lies in the fact that it is monophyletic and not on its particular categorical rank. When I look at a phylogram I perceive all branches as evolutionary species or higher taxa represented by their evolutionary stem species. Farris (1976) has recently discussed the relationships between categorical rank, taxa, and classification which I think makes these relationships clear and which is compatible with both the above discussion and the evolutionary species concept.

Corollary 2.—Separate evolutionary lineages (species) must be reproductively isolated from one another to the extent that this is required for maintaining their separate identities, tendencies, and historical fates. This corollary covers the special case of the biological species definition (Mayr, 1963; Dobzhansky, 1970). The biological species concept stresses the community gene pool and reproductive isolation. Both are inherent in the evolutionary species concept (as Simpson, 1961, concluded). And, in spite of the objections of Sokal and Crovello (1970) and of Ehrlich and Raven (1969), the biological species concept seems a testable special case definition covering the sympatric occurrence of sexually reproducing sister species (species that are each other's closest relatives). Thus, while the biological species concept may be valid it is not inclusive (see Hull, 1971, for a detailed criticism of Sokal and Crovello, 1970).²

² Rosen (pers. comm., and two manuscripts in press) has argued that the biological species concept is simply invalid from the point of view of taxonomy and geographic analysis of monophyletic groups of taxa. This is because its premises are designed to sacrifice evidence of cladistic relationships in favor of real or imagined data on reproductive isolation when the two conflict. If so, one might ask if the concept should be used at all, at least by taxonomists and biogeographers.

Corollary 3.—The evolutionary species concept does not demand that there be morphological or phenetic differences between species, nor does it preclude such differences. Therefore, any investigator may under- or over-estimate the true number of evolutionary species at one time plane or through several time planes when he or she bases that number on morphological or phenetic difference. The phenetic species concept (as discussed, if not explicitly defined, by Sneath and Sokal, 1973) is a special case of this corollary when phenetic differences do occur between separately evolving lineages. The corollary specifically carries the connotation that real evolutionary lineages exist in nature outside man's ability to perceive these lineages (cf. the attitude taken by Dobzhansky, 1970; Huxley, 1940; Mayr, 1963, 1969; Meglitsch, 1954; Ghiselin, 1974; but not Darwin, 1859, or Gilmour, 1940; see Meglitsch, 1954 for a critique of Gilmour's attitude). The under- or over-estimation of the actual number of evolutionary species represents the observational error in the systems or methods employed to differentiate species. For example, it is possible that a fossil assemblage includes two sibling species with identical morphology in their preserved characters, but which operated as separate lineages when living. A paleontologist would conclude, on the basis of the evidence at hand, that only one lineage existed. Thus, he would under-estimate the actual number of evolutionary species. The same investigator might interpret a sexually dimorphic species as two species, an over-estimation. A neontologist might recognize two evolutionary species as a single species because they hybridize at their zone of sympatry, while a future neontologist might conclude that this documented hybridization represented a sorting out and reinforcement of the two species' identities (Dobzhansky, 1970) rather than a swamping of their identities. In practice, as Sokal and Crovello (1970), and others have pointed out, the morphological or phenetic dif-

ferences between populations will usually determine the number of species recognized. But this does not require investigators to accept a phenetic species definition or a phenetic species concept (see Hull, 1971, for discussion of this point). Rather, it requires that an investigator adopt the working hypothesis that sufficient morphological difference combined with geographic distribution are adequate evidence for separate evolutionary lineages. But what is "adequate" evidence? I suggest a clearly stated hypothesis with corroborating instances which are both relevant and parsimonious. What is adequate will change with increased knowledge of organisms studied and experience in dealing with similar problems. If this sounds rather vague, I suggest that no concept or method can guarantee a "correct" solution will follow from it. There is no guard against practicing "bad science" unless "bad" is defined in relation to some authoritarian standard. What is important is that the hypothesis be open to testing.

Corollary 4.—No presumed separate, single, evolutionary lineage may be subdivided into a series of ancestral and descendant "species." This corollary is, perhaps, self-evident and would hardly be worth discussing if it were not for the rather common practice among some paleontologists of subdividing a single lineage into a number of "species." Simpson (1961) viewed this practice as necessary for escaping a kind of infinite regression in classification. He said (1961:165): "If you start at any point in the sequence and follow the line backward through time, there is no point where the definition would cease to apply. You never leave an uninterrupted, separate, unitary lineage and therefore never leave the species with which you started unless some other criterion of definition can be brought in. If the fossil record were complete you could start with man and run back to a protist still in the species *Homo sapiens*. Such classification is manifestly both useless and somehow wrong in principle."

If this were true, then Simpson's definition and the modification presented here would be useless. However, evolution is composed of two geneological processes. One, the continuum, ties all of life together. The other, punctuations of the continuum, produces diversity, when accompanied by differentiation followed by divergence, by providing independence of lineages. As Bonde (1975:294) has stated: "This continuum is subdivided in a non-arbitrary way by the *speciation process which delimits 'natural' species in the time dimension.*" Every punctuation of the continuum followed by divergence results in a single evolutionary lineage being split into two or more evolutionary lineages. There is no doubt that one can run from man to protist in one classificatory taxon, but, in my opinion, that taxon would be Eucaryota, not species *Homo sapiens*. There was a genus *Homo* before there was a species *Homo sapiens*, just as there was a class Vertebrata before any of the Recent vertebrates evolved. Thus, we tie together increasingly ever larger taxa on the basis of the continuum they are hypothesized to have shared in the past, and if we adopt a truly natural classification, this classification will document past continua, not bury their reality or existence.

It is the punctuation of continua which is the first prerequisite that may lead to evolutionary diversity among species at any one time. These punctuations are for the most part what are termed allopatric speciation events (Mayr, 1963, for discussion), but there is no conceptual reason to exclude sympatric speciation as a special case. In the case of the allopatric speciation model, one might expect that in most circumstances the ancestral species would become extinct at the time of speciation. This is because it is improbable that either of the two daughter species would have the same identity, role, and historical fate as the ancestral species. Thus, in most cases the methodological necessity of postulating extinction of ancestral species in phylogeny reconstruction as advocated by Hennig (1966)

is biologically (as well as methodologically) sound. However, an implication of the evolutionary species concept would seem to be that if the ancestral species can lose one or more constituent populations without losing its historical identity or tendencies, then it can survive such a split. For example, there are herpetologists who recognize phenetically different parthenogenic "clones" of uniparental salamanders and lizards as species (Darevsky, 1966; Wright, 1967; Uzzell and Barry, 1971). Darevsky (1966) recognized four uniparental species of *Lacerta* from the Caucasus and suggested their derivation from *L. saxicola*. The uniparental whiptail lizard *Cnemidophorus opatae* is said by Wright (1967) to be derived from the sexually reproducing species *C. tessellatus*. Does this derivation, probably caused by a fortunate mutation in a single female, require that *C. tessellatus* became extinct at the time this female's first brood hatched? I doubt that the origin of *C. opatae* has any more effect on the identity and evolutionary tendencies of *C. tessellatus* than did the death of any one other member of the population. One might argue that such "clones" are not species but variants of a single species (see Zweifel, 1965). Yet, they do represent independent lineages (albeit perhaps of short duration) and thus do correspond to evolutionary species. Another example is the origin of a plant species by hybridization and subsequent polyploidy. This speciation mechanism would seem to have little effect on either parental species (except the waste of some ova and pollen) unless the hybrid successfully outcompeted its parents and caused their extinction, which would be possible only if the parental species survived the actual origin of the hybrid. It might even be reasonable to postulate that the allopatric separation of a peripheral isolate of a large population could occur without initially affecting that large population. The survival of the same species through more than a few of these "buds," however, would appear unlikely because it is unlikely that any one

species could stand the loss of geographically or ecologically unique gene combinations without its role and tendencies being changed. The problem of determining the survival of a particular ancestral species in this situation is the practical testability of the situation. Engelmann and Wiley (1977) have argued that ancestor identification based on morphological or stratigraphic evidence is invalid. If so, it may not be possible at present to separate out those cases where peripheral budding results in extinction of the ancestral species from those cases where it does not. The point I would like to make is that both concepts are compatible whether or not we have the methodological tools to discriminate between them at the present time.

ASEXUAL SPECIES AND ALLOPATRIC DEMES

Asexual species have been the bane of all proposed species definitions that are not overtly typological. Dobzhansky (1970) has termed the asexual species a pseudospecies. Yet, asexually reproducing lineages have existed and do exist. Phenetic taxonomists have, with justification, pointed to the difficulties of applying various biological species concepts to asexual species. Mayr (1963) concluded that his biological species definition was restricted to sexually reproducing species. Simpson (1961) suggested the evolutionary species concept covered asexual species. I suggest that asexual species can be accounted for under the evolutionary species concept in the same way we place allopatric demes into a single sexually reproducing species. We may ask, "why are the Siberian and North American populations of wolverines considered the same species?" (Kurtén and Rausch, 1959). One might answer that we *assume* they would interbreed *if* they were brought into contact. This answer is impossible to evaluate because it assumes some future event. Anything could happen, but only what does happen can be used to corroborate an hypothesis. While such a statement might

be considered a prediction, it cannot be used to justify the deduction. One might argue that there must be migration which keeps the populations from diverging morphologically. There is no evidence at hand for this, just the a priori assumption that they *must* diverge unless some other factor (such as migration) is present. I suggest that Siberian and North American wolverines are considered the same species because we have no corroborating evidence that they have reached a point of divergence where we can deduce that they are following separate evolutionary pathways. It is possible that 1,000 or 10,000 years from now an investigator will see differences and conclude that wolverines are following two independent evolutionary paths. It is possible that wolverines are already differentiated but we have examined the wrong characters for detecting that differentiation. I would suggest that whether wolverines are now differentiated or will differentiate in the future, the decisive factor in this process will be the geographic event which separated them and thus set up their potential independence. But at this time we have no corroboration that this particular geographic event will lead to separate evolutionary paths and thus we have no reason to recognize two evolutionary species. Meglitsch (1954) and Simpson (1961) argued that an evolutionary species definition can be applied to asexual organisms because the populations have retained the capacity to evolve as a unit if artificial (not man-made) barriers are removed, implying the assumption that uniparental lines are derived from biparental lines (Dougherty, 1955; Pontecorvo, 1956; Stebbins, 1960). Perhaps so, but like potential interbreeding, this calls for evidence not at hand. My reasoning above would also apply to predominantly asexually reproducing species. It is not the evolution of asexual reproduction which "permits" us to consider genetically separate clones as a single species, but their lack of significant evolutionary divergence. Any species composed of allopatric demes or

asexual clones has the potential for splitting into two or more separate independent evolutionary species, but it does not follow that any significant divergence *must* occur. Lack of differentiation is as valid a historical fate as differentiation and it may have real genetic, epigenetic, ecological or other bases. We may hypothesize a lack of differentiation even if we cannot distinguish between truly undifferentiated populations and differentiated lineages whose nature has gone undetected. Failure to distinguish between the two represents an inadequacy of our systems of observation and method and not the inadequacy of the concept. In other words, we are faced with the same Type I and Type II errors that plague all systems of hypothesis testing, the chances of rejecting a true hypothesis and the chances of accepting a false hypothesis.

ECOLOGY AND THE EVOLUTIONARY SPECIES

Van Valen (1976:233) recently offered a modification of Simpson's (1961) species definition: "A species is a lineage (or closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range."

Although there is much in this definition and Van Valen's subsequent discussion that I can agree with, the definition has certain logical difficulties. Any species is a component of its environment and must be at least minimally adapted to the biotic and abiotic factors of that environment if it is to survive. Species cannot be divorced from their environment any more than they can be divorced from their gene pools or their morphologies. But, species do not have to occupy minimally different niches or adaptive zones from other species within their ranges to be considered species.³ It is

³ I recognize that the term "adaptive zone" as used by Van Valen (1976) is not the exact equivalent to "niche," but the distinction is irrelevant to this discussion.

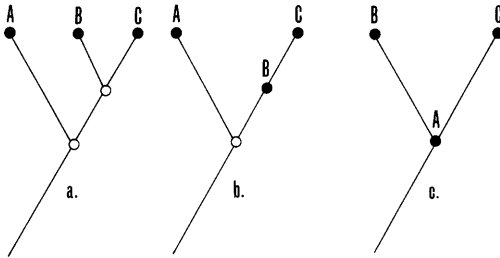


FIG. 1.—(a). One of four possible aspect-B statements of the phylogenetic relationships between species A, B, and C. (b). An aspect-A statement with “species” B considered the direct ancestor of “species” C. (c). An aspect-A statement with species A considered the ancestor of species B and C.

possible for two species to share essentially the same niche within the same range. In the case where resources are not limiting, two such species could co-exist. In the case where resources are limiting, one of the species could replace the other through interspecific competition from that portion of the range where they are sympatric, or, entirely via extinction. Indeed, *if* interspecific competition causes at least some extinctions, it can work only where the niches of the competing species are similar enough for competition to occur or where one species’ niche completely overlaps the other’s (MacArthur and Levins, 1967).

This definition, applied to *successful* species, could be considered another special case definition of the evolutionary species concept as defined above. But, given the original definition of Van Valen (1976) one might argue that a species forced to extinction through interspecific competition was not a species at all. Interestingly, Pitelka (1951) presents exactly this argument in considering a hypothetical scenario involving blue jay evolution. Given the hypothetical situation where the Florida scrub jay and the Texas jay were physiologically incapable of interbreeding, could the Florida jay be considered a species if it should fail to survive when it meets its ecological equivalent and sister species, the Texas jay? (Pitelka, 1951:379). Pitelka suggest-

ed that if the Florida scrub jay were eliminated, then it should not be considered a separate species, in spite of reproductive isolation, because the two jays are ecological equivalents. I would suggest that the elimination of one sister group by another through competition (and not swamping of the gene pool) is corroboration of separate lineages and therefore corroboration of separate species rather than the reverse. Both Van Valen’s and Pitelka’s discussions have merit, but it is my opinion that such concepts lead to an underestimation of the rates of extinction due to interspecific competition.

THE EVOLUTIONARY SPECIES AND PHYLOGENY RECONSTRUCTION

Engelmann and Wiley (1977) argued that ancestor-descendant hypotheses based on morphological or stratigraphic evidence were unscientific because they could never be corroborated or refuted by valid tests. We addressed our discussions largely to alternate hypotheses such as those shown in Figs. 1a and 1b. Figure 1a represents what Nelson (1973) terms an aspect-B phylogeny in which only cladistic relationships are expressed and ancestral species remain hypothetical. Figure 1b represents Nelson’s (1973) aspect-A phylogenetic hypothesis in which, for this example, species B is hypothesized the direct ancestor of species C. If an investigator adopts the evolutionary species concept, then Fig. 1b is logically impossible because “species” B and “species” C are part of the same unitary evolutionary lineage and thus B belongs to the same species as C. Thus, the problem collapses into a two-taxon problem whose relationships are already resolved since A must be the sister species of BC given no other taxa. Of course, population B could be considered ancestral to population C, given that BC is an evolutionary species, since it is a logical deduction that some individuals (sampled or unsampled) from population B are the populational ancestors of all of the individuals of population C (see Engelmann and Wiley, 1977:2, for a discussion of

population ancestors).⁴ I would conclude that much of the discussion we presented was directed toward a problem which does not exist under the evolutionary species concept and which we would not have discussed in the manner we did if we had adopted this concept. However, I would maintain that our analysis of the problem is applicable in cases where it is postulated that one species gave rise to two or more daughter species and itself became extinct (Fig. 1c). I would also submit that in a situation where an ancestral species is evolving phyletically (anagenic evolution) so that the autapomorphies which it will leave to its descendants as synapomorphies are fixed over a period of time, then the problem, on a morphological level, will never be resolved. This is because when the ancestor splits from its own ancestor it will presumably have few, if any, of the derived characters which will be fixed in its own populations at a later time (or times) and left to its descendants when it speciates and becomes extinct. Thus on a morphological level the analysis might result in a species being the primitive sister group of its descendants, plus the ancestor of its descendants, plus the third taxon in a trichotomy with its descendants depending on the rate of phyletic change and the number of samples from various stratigraphic levels available to the investigator. This is because at various times the ancestor might have none, part, or all of the shared derived characters of its descendants. Thus, even if we could identify one part of the lineage as the actual "ancestor," earlier parts of the same species would not be identifiable as the

ancestor in question. Finally, with regard to stratigraphic criteria, if the ancestor can survive the split which produced one or more descendant species, then stratigraphic criteria cannot serve to falsify or corroborate an ancestor descendant hypothesis on the species level, since it is conceivable that an ancestor could post-date its descendants in the fossil record. But, if the ancestor cannot be established on morphological grounds, then perhaps that question is moot.

ACKNOWLEDGMENTS

Earlier drafts of this paper were read by numerous reviewers whose comments are greatly appreciated. These include Drs. Richard Johnston, Robert Hoffmann, and Norman Slade and Messrs. Randall Moss, Gregory Pregill, and David Wiseman (University of Kansas); Drs. George Engelmann, Eugene Gaffney, Norman Platnick, Donn Rosen, and Bobb Schaeffer (American Museum of Natural History); and Dr. Michael Ghiselin (University of California at Berkeley). My special thanks to Dr. David Hull (Univ. of Wisconsin-Milwaukee) and Dr. James S. Farris (State Univ. of New York, Stony Brook) for their extensive and penetrating comments which greatly strengthened the final draft. Ms. Debora Bennett prepared the figure. The conclusions drawn, and any mistakes in logic made, are my own responsibility.

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⁴Of course it is impossible to verify (in the absolute sense) that B is a sample of the ancestral continuum leading to C. But this is, again, a fault of our system of observations and is common to all observational sciences. It is analogous to the wolverine problem and to the problem of "verifying" that similar features are homologous. One could corroborate the hypothesis by showing that a series of intermediate samples between B and C formed a statistically insignificant continuum (as a whole) and could refute the hypothesis by showing the opposite.

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Manuscript received April 1977
Revised August 1977