

Species Concepts, Speciation, and Higher Taxa

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Abstract. The evolutionary species concept appears to be of general applicability in biology and refers to real entities in nature which have many of the properties of individuals. Analogies between such species and higher taxa lead to the conclusion that distinct monophyletic higher taxa, whether holophyletic or paraphyletic, form similar entities, may be more individual-like than holophyletic groups which include diverse subtaxa, and may thus be considered to be more natural than such taxa.

Throughout history, it seems to have been a fundamental characteristic for man to recognize different species (or kinds) amongst the organisms with which he interacts. Even today, societies that are regarded as primitive in many respects use classifications which may be highly sophisticated and are predominantly based on units that correspond to those which trained biologists generally consider to be species (Berlin, 1973; see also Berlin *et al.*, 1974, and Hunn, 1977, for detailed examinations of such systems amongst the Tzeltal-speaking people). Despite this impression of a general ability to recognize species, there has been much disagreement on what species actually are. As a result of increases in knowledge and changes in perspective, there have also been changes in species concepts (Simpson, 1961; Mayr, 1969; Wiley, 1981a). This paper does not aim to repeat previous surveys in order to formulate the best concept, and therefore does not refer to much of the literature on the topic, but I will briefly point out the weaknesses of many of the concepts and suggest that one of them appears to be of greatest general applicability. The implications embodied in the nature of species, as well as the processes of speciation and their effects on the ancestral species, may be extrapolated to higher taxa. I hope to show that acceptance of the status of species in evolutionary terms as individual entities necessitates the acceptance of discrete monophyletic higher taxa as analogous natural units. I must admit at the outset that many, if not most, of the ideas in this paper are not new, but it seems that they have not previously been fully integrated and explored with respect to their implications for the recognition of taxa at various levels of the taxonomic hierarchy.

The first point that must be clarified before species concepts can be evaluated is whether species (as taxa) are entities which have an actual existence in nature, independent of man as an observer, or whether they are imaginary constructs formulated to facilitate his subjective organization of the phenomena he observes around him. In other words, are species to be viewed from an ontological or an epistemological perspective? If the former, then a species must be considered to be an entity that may be discovered and recognized (and perhaps named) with greater or lesser success, depending on

whether suitable techniques have been applied. Such species exist, whether we can recognize them or not, and the naming of such a species represents a hypothesis that the named unit corresponds to an actual entity in nature. If species are considered to be imaginary constructs, however, the naming of a species cannot be regarded as a hypothesis, even if generally agreed criteria are used in its recognition, but is merely a statement reflecting the mental state of the investigator. The naming of an 'ontological' species is a stage in what may be a series of observations and experiments designed to test the validity of the hypothesis, whereas the naming of an 'epistemological' species has no further implications. The whole of natural science has an ontological basis, and this is true of systematics also, as has been pointed out by Griffiths (1974). At the population and species levels the success of evolutionary explanations for the phenomena observed is a further indication that the entities involved almost certainly have some existence independent of our abilities to recognize them. Species must thus be considered to be real (ontological) entities.

The ontological nature of species has the corollary that such entities are, or at least have many of the properties of, individuals (Griffiths, 1974; Ghiselin, 1975; Hull, 1976). This idea is gaining wider acceptance and will be discussed more fully below. By contrast, if species are entirely epistemologically based, they must be classes, the membership of which is defined by the possession of essential characteristics specified by man. The existence of a class of objects depends on the definition or specification of the essential features required for membership in the class, and such definition depends entirely on the imagination of man. This means that classes have no existence independent of man's thinking, and thus cannot form real units in nature.

If one wishes to evaluate the various species concepts that have been used, then they must be approached from the perspective of their applicability to real 'individual' entities in nature. Since such entities may be of various sorts, some workers have regarded the search for a single generally applicable species concept as doomed to failure. Nevertheless, if such a concept could be found, one applicable to all of the various types of species that may exist, each of these being a special case

within a general condition, then such a concept would be of far greater usefulness than a number of different concepts. This is particularly true in systematics, since this is the area of biology that serves to integrate all other fields of investigation. The major concepts that have been suggested in the past may be evaluated with this aim in mind. It should be noted in passing that a species concept is a class definition, comprising a specification of the essential characteristics that determine whether a particular individual entity is admitted to membership of (i.e., is recognized as belonging to) the class 'species' (as a taxonomic category) or not.

Viewed from the ontological perspective, Lewin's 'three species concepts' (Lewin, 1981) represent successive approximations to the true situation in any particular instance, and could thus apply to any concept which treats species as ontological entities. His third 'concept', the species as designated by a specific name, is the starting point which may be refined to correspond to the second, the species as we perceive it, which in turn may be further tested so as to correspond as closely as possible to the species as perceived by the organisms themselves (i.e., the actual unit in nature). These 'concepts' are thus different in kind from the other concepts to be considered. The typological and nominalistic concepts (see Mayr, 1969) view species as classes, and are thus not applicable to real species. The morphospecies (Cain, 1963), if applied strictly without further implications, also involves a class concept. The palaeospecies (Cain, 1963), sometimes termed sequential species, involves the arbitrary subdivision of a single lineage into different species over time; because the boundaries between such species usually correspond to accidental gaps in the fossil record and not to any actual biological discontinuity, they cannot reflect the existence of units in nature. The biological species (Mayr, 1969) refers to real units in nature but is restricted to sexually reproducing organisms. The same limitation applies to Ghiselin's (1975) refinement of it (couched in terms of reproductive competition) and Paterson's (1979) change of perspective from reproductive isolation to specific mate recognition. The agamospecies (Cain, 1963) only refers to asexually reproducing organisms.

The single principle that governs the existence of all species as real units in nature is evolution, so that a species concept which is founded on this may be applicable to all organisms. Such a concept was formulated by Simpson (1961) and refined by Wiley (1978), whose definition is as follows: '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.' (Wiley's paper should be read for a more complete justification of this concept.) Although the criteria to be used in testing the applicability of this concept in any particular case are not stated in the definition (i.e., it is theoretical rather than operational), this is no disadvantage because it means that the definition does not have to be changed if new criteria are found, and it also has greater heuristic value than an operational definition (Hull, 1968; Ashlock, 1980). Any and all criteria

that may theoretically be used to estimate the genealogy and identity of a particular hypothesized species may be used in practice, whether these be genetic, ecological, behavioural, morphological, etc.

Wiley (1978) suggested that there are at least four corollaries which follow from acceptance of an evolutionary species concept: 1) every organism, past or present, belongs to (forms part of) some evolutionary species; 2) species must be reproductively isolated (through the operation of isolating mechanisms, specific mate recognition systems or any other means) to the extent required to maintain their distinctness; 3) species may or may not exhibit recognizable phenetic differences (but they almost invariably do, although such differences may sometimes be difficult to detect; in the case of sexually reproducing organisms, for example, species must minimally differ in some aspect of their mate recognition systems, Paterson, 1979); 4) no single lineage may be subdivided into a series of ancestral and descendant species (rejection of palaeospecies, as above). Wiley also maintained that such an evolutionary species concept applies equally to sexually and asexually reproducing organisms, because evolutionary processes give rise to lineages in either case. Indeed, there is a strong analogy between asexual species and completely allopatric demes of sexual species, the clones and demes not being linked by mating bonds.

One may thus visualize a continuum from species that are entirely sexual and show gene flow between all parts of the species (Fig. 1a), to those that have reduced gene flow between some populations (Fig. 1b), to those that have no gene flow between some populations (Fig. 1c), to those that have occasional sexual interchange amongst some parts but are predominantly asexual (Fig. 1d), to those that are entirely asexual (Fig. 1e). All are real evolutionary species, but their recognition depends on different criteria, the strongest being genetic or reproductive (at the sexual end of the continuum), but these of necessity being replaced by purely phenetic criteria at the asexual end. As Wiley (1981a: 36) has so clearly stated, 'The similarity exhibited between two completely separate demes . . . rests upon the same factors that give cohesion to an asexual species, likeness produced by a stabilized epiphenotype and parental links.' Such similarity can be estimated only by phenetic criteria, whether morphological, behavioural, karyological, ecological, etc.

If species are accepted as individual evolutionary lineages, then speciation must involve the formation of new individuals. There are various ways in which this may occur, and I do not intend to review them here (this has been done by many other authors, such as Grant, 1971; Bush, 1975; White, 1978; Futuyma and Mayer, 1980; Paterson, 1981). In general, however, it seems that most new species arise as a result of some change in a relatively small part of the parental species, which causes an alteration in the characteristics of that part such that it establishes its own evolutionary identity and tendencies and escapes the homeostatic constraints of the parental species. Such changes may take place relatively rapidly, after which the new species be-

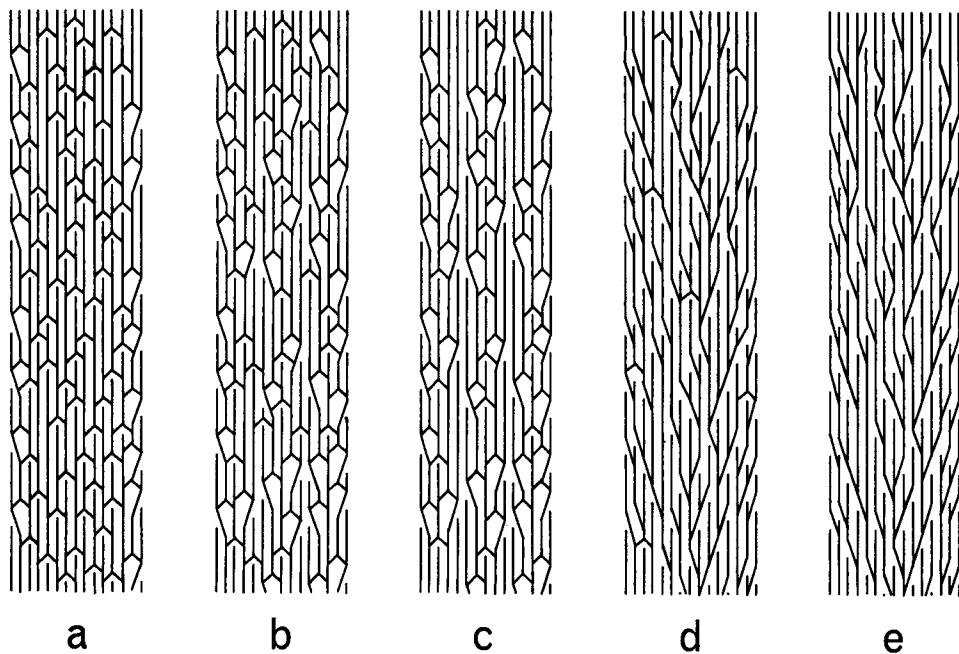


Fig. 1.

comes stabilized in its environment, as has been pointed out by Eldredge and Gould (1972) and others. Such speciation may be represented as in Fig. 2 for the extremes and centre of the continuum of species types shown in Fig. 1. (The 'punctuated equilibria' model has been adopted for clarity of illustration, but it should be noted that all subsequent arguments apply equally well to 'phyletic gradualism', in which change is less abrupt.) Other kinds of speciation, such as reticulation resulting from fusion of parental species or parts of them, or the occurrence of polyploidy, operate under strict constraints, are probably far less common, and have no real relevance to the subsequent discussion although they do not invalidate it.

Fig. 2 shows that the ancestral species seems to have been changed minimally by the production of the daughter species; it still appears to have the same evolutionary tendencies and identity after the speciation event as before it. This is not surprising, because only a relatively small part of the parental gene pool became diverted. (If the two parts of the gene pool which became separated were about equal in size, then one might expect that the evolutionary tendencies of both would be changed, but such a situation is statistically improbable and seems to have been uncommon.) It thus appears that there are generally no *biological* grounds for considering that an ancestral species necessarily becomes extinct upon producing a daughter

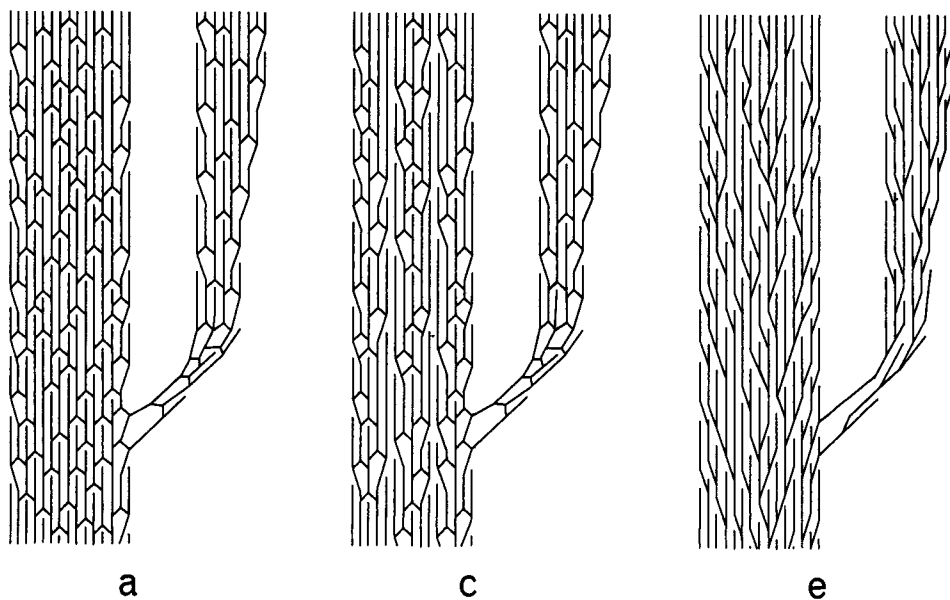


Fig. 2.

species, a conclusion which has already been reached by various other authors, such as Bell (1979) and Wiley (1981a), although this is a *logical* requirement of a strictly cladistic classificatory approach (Hennig, 1966).

According to Wiley (1979), 'the [evolutionary] species . . . is considered monophyletic [= holophyletic] by virtue of its individual nature.' Like Holmes (1980), I can see no justification for that view, and I would suggest that consideration of it can provide some useful insights. Tuomikoski (1967) and Van Valen (1978) also considered this aspect, and both concluded that a persistent species that has given rise to a daughter species must be considered to be paraphyletic because it no longer includes all descendants of the common ancestor. (I do not wish to reopen the debate on the definitions of terms connected with monophyly, but will refer to the concepts as defined by Holmes, 1980, such that monophyly includes both holophyly and paraphyly.) In the case of a sexually reproducing species consisting of a single interbreeding population (Fig. 2a), this is perhaps stretching the point a bit far, since the various parts of the species are linked by mating bonds. It is thus not possible to subdivide it, which is perhaps why Wiley and Holmes have considered that the application of terms such as 'paraphyletic' are not appropriate in the case of species. When we examine asexually reproducing species and species consisting of allopatric demes, however, a different picture emerges (Figs 2c, 2c). Since there is no gene flow between the clones and demes, such a species appears to be made up of a series of lineages (most obvious in Fig. 2c if viewed obliquely from below), and it is only recognized as a unit because of its phenetic cohesion. Indeed, Wiley (1981a: 36) implied that an evolutionary species that consists of clones or allopatric demes is made up of a series of lineages rather than a single lineage. Acceptance of this necessitates a modification of the definition, as follows: *A species is a single lineage or minimal monophyletic group of lineages of ancestor-descendant populations which maintains its identity from other such lineages or groups of lineages and which has its own evolutionary tendencies and historical fate.* Note that this definition specifies that such an entity must have a unique origin (be monophyletic) but also permits such a unit which consists of clones or allopatric demes to be recognized as valid even if it has persisted after a speciation event and is thus paraphyletic. Willman (1983) has pointed out that no species is holophyletic. He has also emphasized the possibility of polytypic species being paraphyletic, with one of the included subspecies being more closely related genealogically to another species than to the other parts of the same species. He rejected the application of the word 'paraphyletic' in this instance, however, because he was considering only sexually reproducing species with pervasive mating links between all included organisms. (Willman's paper should be consulted for further details, including some difficulties with the application of cladistic principles in such cases.)

The acceptance of an evolutionary species concept, including its implications for speciation and the recognition of the paraphyletic nature of at least some per-

sistent ancestral species, has implications for the recognition of higher taxa. These implications have apparently not been fully appreciated, although Mishler and Donoghue (1983) have suggested that many species are more similar in kind to higher taxa than has generally been accepted. We can exclude the phenetic school from consideration at the outset because the taxa recognized in that approach are epistemologically, rather than ontologically, based and thus do not necessarily even approximate to the actual units existing in nature (see Dunn and Everitt, 1982). The same applies to the so-called transformed cladistic school, where the estimation of an actual evolutionary pattern is considered irrelevant (Platnick, 1980; Patterson, 1980; Charig, 1982). (This does not imply that the patterns of character distribution discovered by practitioners of these schools do not actually exist, but rather that such patterns themselves are considered sufficient for classificatory purposes; the patterns are not analysed further in terms of the likelihood of their reflecting actual evolutionary events.) Both the phylistic (= evolutionary, Holmes, 1980) and Hennigian ('phylogenetic') cladistic schools purport to recognize units which are based on estimates of the actual branching patterns and units involved in evolution, however, and so both must be considered.

Although the phylistic school includes various different approaches, mainly involving aspects of the inclusion of fossils, as Holmes (1980) has emphasized, the minimal difference between it and the Hennigian school is that of the recognition or not of paraphyletic groups. Thus, phylists recognize groups, each of which is derived from a single common ancestor (which is included in the group), which may or may not include all of the descendants of that ancestor, and which is delimited on the basis of distinctness (phenetic gaps) from other related groups. Hennigian cladists recognize similar groups but specify that all descendants must be included in the group and exclude any criterion of phenetic distinctness. The differences in approach are illustrated in Fig. 3. Justification for the Hennigian cladistic approach is found not only in its logical basis (the classification reflects the branching sequence exactly) but also in the idea that because a holophyletic group represents all the descendants of a single lineage and therefore the results of a single evolutionary event, such a group is spatiotemporally restricted and may thus be considered to be an 'individual', 'historical group', or other similar real entity rather than a class (Hennig, 1966; Griffiths, 1974; Patterson, 1978; Ghiselin, 1980; Wiley, 1980, 1981a). By contrast, they consider paraphyletic (and polyphyletic) groups to be classes, and thus not natural. (Note that this use of 'natural', from Van Valen (1978) and Wiley (1981a) differs from that of many other authors, especially pheneticists, and implies the existence of such a unit in nature. It seems to correspond more closely to an intuitive meaning of the word, is ontologically based, and is therefore to be preferred.) Polyphyletic groups are obviously classes because their members do not have a unique and common evolutionary origin, so they may henceforth be ignored.

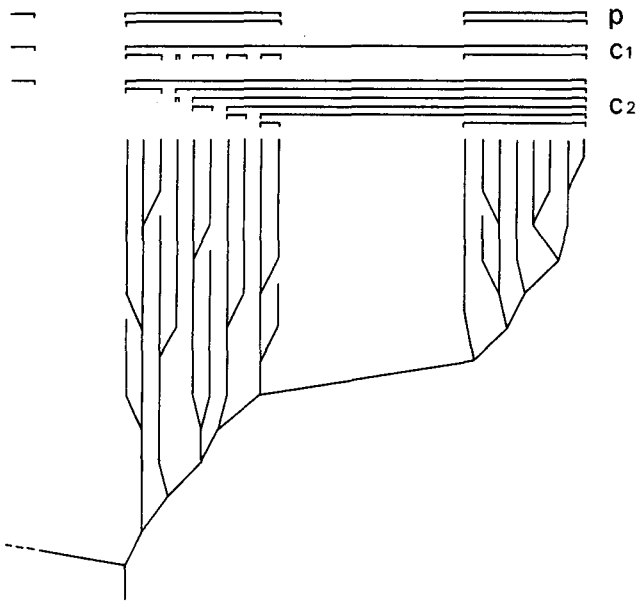


Fig. 3.

But paraphyletic groups do have unique origins, so they may qualify as natural units and need to be considered further.

One reason for the rejection of all paraphyletic groups in the past appears to have been a rather imprecise concept of which such groups may legitimately be recognized in a phyletic classification. It has been claimed, for example, that 'invertebrates' or 'animals' are typical paraphyletic groups (Hennig, 1975). Although they are certainly paraphyletic, they are highly unlikely to be recognized formally in a phyletic classification, because there are phenetic gaps within these groups that are much greater than the gaps separating them from 'vertebrates' and 'man' respectively, as has been pointed out by Ashlock (1980). (The objections of Platnick (1980) and Patterson (1980) to recognition of paraphyletic groups because they are 'defined' by the absence of characters are consequences of the transformed cladistic approach, which does not aim to make evolutionary sense and so may be dismissed in the present context.) For legitimate recognition in a phyletic scheme, a paraphyletic group must have a similar degree of cohesion (range of phenetic variation) to that possessed by other related monophyletic groups recognized at the same taxonomic level and must be separated from such groups by gaps greater than any gap occurring within the group, i.e., paraphyletic groups must form grades, or 'delimitable and persistent anagenetic units' (Huxley, 1957). Just as there are some holophyletic groups which are not particularly interesting and which are thus unlikely to be recognized formally (although the presumed maximum benefits of the cladistic system as regards information content and stability (see Mickevich, 1978) are only achieved when all such groups are used and the classification is thus fully resolved (Colless, 1981)), so there are paraphyletic groups which are not utilized for the same reason. Wiley (1981a: 243–250) rejected the use of gaps for de-

limitation of groups because they are likely to disappear as intermediate forms (particularly fossils) are discovered, with the result that the classification will change if it is a phyletic one (but will not change in essentials if it is a cladistic one). This may hold in some instances, but I doubt that it will be a significant problem in practice. Apart from anything else, there is no reason why the phyletic classification should change any more than the cladistic one if use is made of the convenient and hierarchically ambiguous category of 'plesions' in both cases. Wiley's main objection seems to be that he feels that the recognition of gaps 'obscures the phylogenetic relationships of the historical course of speciation' (1981a: 250). If the only function of a classification is to reflect genealogy, then his objection is valid, but the phyletic approach goes beyond that in attempting to estimate the relative significance of the various branching events by reference to the distribution of evolutionarily important characters, and to reflect only those that have produced significant gaps.

It is necessary to examine the concept and characteristics of an 'individual' further in order to evaluate the status of paraphyletic groups in this respect. Hull (1976) characterized individuals as 'reasonably discrete, spatiotemporally continuous and unitary entities'; such entities have parts, not members, and they can be named and described but not defined; their 'unitary' quality (cohesion) does not depend on the unifying effects of external causes alone but has some intrinsic basis. Various authors have maintained that these characteristics require that individuals must participate in natural processes as units, and that natural individuals above the organism level must therefore evolve as units. Species have been considered to fulfil this requirement. Only species that consist of a single interbreeding population (deme) or groups of such populations that show significant gene flow between them are capable of fulfilling such a unitary evolutionary role, however. Sexual species comprising allopatric demes and asexual species, which together may very well be the most common types, need not function as such units. The requirement of unitary participation in evolution would necessitate that only species which fall at one end of the continuum (Fig. 1a) may properly be considered to be individuals. Hull (1976) has already questioned whether all species have the unity necessary for them to participate in processes as units, and he went further in a later paper (Hull, 1980) in suggesting that many 'species' are so different in type that they should not be considered as equivalent, for this very reason.

Reed (1979) examined the concept of species as individuals from a different viewpoint, that of symmetry operations, according to which species may be envisioned as 'dynamic entities defined by their relative stability in the face of various processes' such that they exhibit 'invariant patterns of change'. As I understand it, this means that a particular species shows cohesion and continuity such that even under diverse environmental conditions its epiphenotype remains relatively constant over short periods of time, but the pattern of change in epiphenotype resulting from processes involving origin

(‘birth’), adaptation to long-term environmental changes (‘development’) and eventual extinction (‘death’), is a constant feature of all species. (I have extended Reed’s analogy with the life cycle of an organism by including the terms in parentheses.) The intrinsic basis that is responsible for such ‘relative stability’ and ‘pattern of change’ is, of course, the genetic material, which not only limits the amount of variation possible at any one time but also permits ordered change over time, since all parts of the species have derived their genetic material from that of the single ancestral entity which established the species (formed the first part of it). Not only do sexual species with pervasive mating links show such characteristics, but so do asexual species and species comprising separate demes, and on this basis they may be considered to be individual ‘symmetries’. If it is thought desirable to limit the ‘individual’ concept strictly to an entity that participates as a unit in natural processes, then species that do not fulfil this criterion may be considered to belong to some different type of unit (perhaps the ‘historical entity’ of Wiley, 1980), being not quite an individual but also definitely not a class. This does not appear to aid in their treatment, however, so that I prefer to accept a slightly broadened concept of an ‘individual’ (at least in the context of systematics) as referring to any entity which exhibits such ‘relative stability’ whether or not it perpetuates the amplification of Wiley’s (1978) species concept corollaries. Not only must a species be reproductively isolated from others (corollary 2), but it must also possess some intrinsic mechanisms whereby its cohesion or ‘stability’ is maintained, regardless of the existence of other species. (This is a change in perspective similar to that involved in Paterson’s 1979, emphasis of specific mate recognition systems as opposed to reproductive isolating mechanisms in sexual species.)

Van Valen (1976) indicated some points in which even the most unitary of species seem to have various properties of classes. Thus, although scientific laws can refer only to classes, and not to particular individuals, it appeared to him that the formulation of laws which refer to particular species was possible. Van Valen gave the example of anthropological laws which refer to *Homo sapiens* (e.g., ‘Rapid culture change produces personality disorientation’). Whether such statements are to be regarded as ‘laws’ rather than mere descriptions of the characteristics of the individual seems doubtful. Such a statement appears to have the generality of a law merely because all parts of *Homo sapiens* are very similar at this time. Given the possibility that the species may evolve and change in the future, there is no reason to suppose that such a ‘law’ will apply equally to the changed conditions at that time—man may have been able to adapt to the point where rapid culture change has no such effect. Van Valen (and others such as Enghoff, 1975) also suggested that species which have arisen through hybridization do not have a single ancestor, but this is not strictly true since such a species has generally arisen from a single hybridization event or at most a few such events which produced a single popu-

lation. The existence of that single ancestral population (or organism) which established the lineage is the critical factor, rather than the actual mode of origin of the ancestor.

Vrba and Eldredge (1984) have pointed out that another characteristic of biological individuals is that they ‘give birth to others of like kind’ and that ‘each more complex individual develops from a smaller number of subparts’. So, organisms reproduce and each new organism develops from a single cell; species speciate and each new species arises from a single population. This also means that only a small subpart of any individual is involved in the production of a new individual. The single cell that develops into a multicellular organism was originally a small subpart of another organism, and the population that forms a new species was a small subpart of another species, a situation already referred to above (see Fig. 2). A corollary is that every individual persists as an essentially unchanged individual after giving ‘birth’. If it is accepted, as is maintained by Vrba and Eldredge (1984) and other cladists, that the only entities forming valid higher taxa are holophyletic groups, then these characteristics of birth and development are not shown by higher taxa. (By definition, a holophyletic taxon cannot give rise to another and yet retain its holophyletic identity, which is the reason for Willman’s (1983) statement that a species cannot be holophyletic.) Examination of Fig. 3 will show, however, that a monophyletic taxon may give rise to another monophyletic taxon, with the new taxon developing from a ‘smaller number of subparts’ (a species in this case), which was originally a small subpart of the ancestral taxon, and with the original monophyletic taxon persisting after the ‘birth’. The ‘production of descendants of like kind’, given as a characteristic of all members of the genealogical hierarchy except for holophyletic taxa by Vrba and Eldredge (1984), is thus characteristic of monophyletic higher taxa also (as long as paraphyly is permitted), which supports their recognition as valid taxonomic units.

Wiley (1981a: 75) maintained that ‘there is no ongoing process which gives a natural higher taxon cohesion’, and he thus concluded that such taxa cannot strictly be considered as individuals but should rather be termed ‘historical groups’. This follows necessarily from his contention, incorrect in my view, that only holophyletic taxa are natural, because such taxa may include phenetically (and thus functionally) varied subgroups (Fig. 3c). If, however, only phenetically distinct monophyletic groups, whether holophyletic or paraphyletic (Fig. 3p), are considered, it seems that such cohesion (or ‘relative stability’) may be present. Such a taxon shows a limited range of variation because of the absence of significant differences in the genetic and epigenetic systems that govern the epiphenotypes of its components. This is entirely analogous to asexual species, the separate clones of which are considered to be a single species because of ‘their lack of significant evolutionary divergence’ (Wiley, 1978). The same applies to allopatric demes of a single sexual species, as was pointed out above. Should there be some significant

change in a lineage such that it (and its daughter lineages) breaks out of the relative stability or cohesiveness shown by its ancestral group, then such a lineage forms a legitimate higher taxon on its own. The fact that a lineage has diverged so significantly has no effect on the (paraphyletic) taxon from which it was derived, however, since the stabilizing processes that operate to maintain the relative constancy of the ancestor are not affected (cf. Figs 2e, 3p). It should be noted that I consider that evidence of 'stability' or 'cohesion' and significant departure from such stability must be sought by reference to the epiphenotype of the taxon, rather than the 'epigenotype' or gene pool, because it is the epiphenotype that is most directly subject to the influences of natural processes (although itself limited by the genetic and epigenetic program). It is for this reason that I would consider Hominidae and Aves as legitimate taxa distinct from their paraphyletic closest relatives, Pongidae and Reptilia. They both show significantly changed epiphenotypes when compared with those relatives, despite the fact that there is less genetic difference between Hominidae and *Pan* or between Aves and Crocodylia than there is within the Pongidae and Reptilia respectively (Wiley, 1981a: 263). Similar reasoning appears to have led to Carroll's (1982) acceptance of a paraphyletic reptilian taxon, Protothyridae. This is different from the genetically based approach of Mayr (1969, 1974) and others, but seems to relate more directly to the situation in nature because it is the total phenotype that is actually the functional and interactive module in nature.

Because monophyletic higher taxa that are epiphenotypically distinct ('adaptively unified groups', Van Valen, 1978), whether holophyletic or paraphyletic, show qualities of 'relative stability' and 'cohesion' in addition to their unitary origins, and also produce descendants of similar type, they seem to be more natural (by virtue of their possession of more of the properties of individuals) than are epiphenotypically diverse holophyletic groups, which have unitary origins but lack cohesion and cannot produce descendants. This conclusion is also implied by Van Valen (1978), although adaptation may play a lesser role than he suggests. Such a view of natural higher taxa should be of maximal general usefulness in systematics. (I say this despite the fact that such taxa may strictly be 'inconsistent' with the branching pattern of the phylogeny on which they are based, as shown by Wiley (1981b). The inconsistency results because the recognition (delimitation) of such taxa is made by reference to information additional to the branching pattern, which has the effect of collapsing some of the branches to the point that they are considered irrelevant and so are not reflected in the classification.) Such a view also clarifies various problems with the nomenclature of natural higher taxa, as I have indicated elsewhere (Brothers, 1983), in that they may be named and described but cannot be defined. Since the basis of this viewpoint rests in the acceptance of an evolutionary species concept, the above definition of that concept may be adapted to apply to natural higher taxa as follows: *A natural higher taxon is a single evolutionary species or a monophyletic*

group of such species which exhibits relative epiphenotypic constancy and distinctness from other such species or groups of species and which has its own evolutionary tendencies and historical fate. This is essentially equivalent to Ashlock's (1980) definition but has the advantage of emphasizing the individualistic nature of such taxa.

As with all theoretical definitions, the problem remains as to which procedures should be followed in applying the above definition and what degree of distinctness (size of gaps) should be considered appropriate for recognizing the limits of taxa in any particular case. Although various suggestions for estimating distinctness have been made (e.g., Brothers, 1975; Michener, 1977; Cherry *et al.*, 1982), the development of such methods remains one of the greatest challenges facing systematists who wish to use a phyletic approach. It remains my view, however, that a strictly derived cladogram must form the basis of any such approach, and that the estimation of phenetic gaps must be done within the constraints posed by such a cladogram, so that the holophyletic and paraphyletic groups that are recognized will be those most likely to function as units in nature. In this way, a purely genealogical diagram (cladogram) may be transformed into a tree-of-life diagram (contrary to the opinions of Sluys, 1984), which is a more complete reflection of the evolutionary history and functionality of the group. It must be noted that Wiley's (1981a: 79–82) rejection of phenetically (and genetically) based taxa defined purely by measures of overall similarity is not in conflict with the above concept of phyletics. Wiley conceived of such taxa as sets (not individuals) defined by characters without reference to other taxa. The phyletic approach advocated here regards taxa as individuals that are recognized by the distribution of characters across a larger grouping such that the individuals have the properties referred to above and are thus distinguishable from each other.

The fact that it may be very difficult, or in some cases even impossible, to delimit higher taxa with absolute certainty is no reason to reject an approach which aims for such delimitation. After all, even at the level of those paradigm individuals, organisms, it is sometimes unclear as to whether one or more is involved, as has been pointed out by Gould (1982) in a discussion on Siamese twins. If uncertainty is present at that level, how much more likely is there to be difficulty at the more diffuse levels of multiorganism systems?

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ADDENDA

Species and Speciation
Transvaal Museum Monograph No. 4
E. S. Vrba, Editor

Insert the following figure captions on pp. 37 & 39 (D. J. Brothers)

Fig. 1. Diagrammatic representation of species with different degrees of sexual interchange and asexual reproduction. Time proceeds upwards. **a** = entirely sexual with regular mating links throughout. **b** = entirely sexual with reduced mating links between some parts. **c** = entirely sexual with no mating links between some parts. **d** = occasionally sexual but predominantly asexual. **e** = entirely asexual.

Fig. 2. Diagrammatic representation of speciation by ancestral species with different degrees of sexual interchange and asexual reproduction. Time proceeds upwards. Letters apply to ancestors as for Fig. 1. Note that in **a** and **c** more lineages, and in **e** more or fewer lineages, could be involved in the speciation event.

Fig. 3. Diagrammatic representation of higher taxa recognized for the phylogeny shown. Time proceeds upwards and relative epiphenotypic divergence is shown horizontally. Recognition of the holophyletic group to the right is taken as the starting point. Each set of horizontal brackets shows the groups which would be recognized at the same taxonomic level using a phylistic approach (**p**), a cladistic approach with sequencing (**c**₁), and a cladistic approach with subordination (**c**₂). Note that in both cladistic approaches, groups with very different ranges of epiphenotypic variation are recognized at the same level, whereas in the phylistic approach the groups are similar in their epiphenotypic ranges. (See Wiley (1981) for conventions allowing the incorporation of extinct and ancestral species into the Linnaean hierarchy.)