

Species concepts and phylogenetics

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Contents

Abstract	page 353
Introduction	354
Historical and ahistorical concepts of species	355
Historical concepts of species	355
Lineage-based concepts	
Hennigian species concept	
Evolutionary species concept	
Genealogical species concept	
Pattern-based concepts	
Monophyletic species concept	
Phylogenetic species concept	
Neophylogenetic species concept	
Individual organism species concept	
Elements of the problem	358
Species and monophyly	
Tokogeny and phylogeny	
Taxa and the unit of evolution	
Pattern and process	
Species as individual organisms and exemplars	366
Species as conjectures	367
Acknowledgements	371
References	371

Abstract

Concepts of species proposed within the phylogenetic paradigm are critically reviewed. Most so called ‘phylogenetic species concepts’ rely heavily on factors immaterial to phylogenetic hypotheses. Thus, they have limited empirical content and offer weak bases on which to make decisions about real problems related to species. Any workable notion of species relies on an explicit character analysis, rather than on abstract properties of lineages, narrative predications and speculations on tokogenetic relationships. Species only exist conjecturally, as the smallest meaningful units for phylogenetic analysis, as based on character evidence. Such an idea considers species to be conjectures based on similarity, that are subsequently subject to testing by the results of analysis. Species, thus, are units of phylogenetic analysis in the same way as hypotheses of homology are units of comparable similarities, i.e. conjectures to be tested by congruence. Although monophyly need not be demonstrated for species-level taxa, hypotheses of relationships are the only basis to refute species limits and guide necessary rearrangements. The factor that leads to recognition of species is similarity in observed traits. The concept of life cycle is introduced as an important element in the discussion of species, as an efficient way to convey subsidiary notions of sexual dimorphism, polymorphism, polytypy and clusters of diagnosable semaphoronts. The notion of exemplars is used to expand the concept of species-as-individual-organisms into a more generally usable concept. Species are therefore proposed for a *diagnosable sample of (observed or inferred) life cycles represented by exemplars all of which are hypothesized to attach to the same node in a cladogram, and which are not structured*

into other similarly diagnosable clusters. This definition is character-based, potentially testable by reference to a branching diagram, and dispenses with reference to ancestor-descendant relationships or regression into population concepts. It provides a workable basis on which to proceed with phylogenetic analysis and a basis for that analysis to refute or refine species limits. A protocol is offered for testing hypotheses of species boundaries in cladograms.

... all things happen to us precisely, precisely now.
Centuries upon centuries and only in the present
do facts happen.

Jorge Luis Borges

When sophistication loses content, then the only
way to keep in touch with reality is to be crude
and superficial. This is what I intend to be.

Paul Feyerabend

Introduction

The concept of species ranks along with that of homology as the most extensively discussed subject in the history of biology. The roots of the species concept, as most biologists understand it today, can be traced back to the 17th and 18th centuries. Early works such as Ray (1686) and Buffon (1749) still strike today's reader as unexpectedly modern by current standards. The same is true of the later works of Geoffroy Saint-Hilaire (1859) and Trémaux (1865; see Nelson, 1989b). The species controversy kept a high profile during the neo-Darwinian period (Slobodchikoff, 1976) and has gained renewed attention in the phylogenetic paradigm. The advent of cladistics resulted in the proposal of a number of new species concepts, with the resulting schisms falling along familiar lines. Published symposia on species concepts still occur regularly (e.g. Davis, 1995). For some, the subject has appeared in print so profusely that it has reached the point of looking worn out, though far from cleared up in content. In fact, the species problem "has never dropped from sight in the long history of systematics" (O'Hara, 1993: 231). Discussions on species definitions scale down to fundamental concepts in comparative biology, systematics and evolution. As these notions change with progress in the field, the idea of species requires reform as well.

Much of the copious literature available on species concepts is highly theoretical in scope, and places disproportionate emphasis on verbal machinations attempting to fit biological concepts into philosophical definitions, or vice versa. While it is certainly

useful to provide a philosophical framework to better define scientific problems, as the recent history of systematics itself demonstrates, a strange imbalance is evident in the literature on species. Much discussion seems concerned exclusively with abstract aspects of the concept, while its biological significance is neglected. Indeed, it seems that little has been accomplished in theory and practice in the long history of philosophical discussions on species. One of the most praised accomplishments of that discussion, the idea of species-as-individuals, is hailed by some as the individuality "revolution" (Ghiselin, 1987). Others, however, view it with less enthusiasm: "Several workers ... typically portray species-as-individuals as crucial to evolutionary biology, although they have been slow to produce cases in which biological problems might be solved better by applying this concept than by ignoring it" (Farris, 1985: 197); or "it [Ghiselin's theory] lacks the empirical basis necessary for a theory to be constructively addressed" (Nelson, 1985a: 388); or still "...the idea of species-as-individuals is marginal to empirical science" (Luckow, 1995: 596).

Obviously, the philosophical delvings of biologists and philosophers into the species problem have been poor in results relevant to those who describe, revise and formulate hypotheses of interrelationships among actual species of organisms. McDade (1995), in a survey of recent botanical systematic monographs, found a majority of works not to discuss the concepts or criteria used to delimit species. The inescapable conclusion is that "many monographers find the species controversy to have little practical bearing on their work" (McDade, 1995: 613). The situation is probably no different in zoology and other subdisciplines. Clearly, the community of practising systematists is starved of proposals with empirical content, and at the same time overfed with abstract formalism about species concepts. Not surprisingly, the minority of monographers who did discuss the subject, for the most part, explicitly based their decisions on observable patterns of differentiation, regardless of the variety of underlying processes supposed to explain them (McDade, 1995: 613). Models relying on narrative predications and metaphysical assumptions,

however elaborate, have proven to be of little use. A need for objective pattern-based strategies to deal with species is evident.

In this paper, I discuss the species problem within a phylogenetic framework. My general guideline is that the species controversy will benefit from adopting an explicit pattern approach. I suggest ways to implement that, by a combination of previously proposed ideas and some new ones.

Historical and ahistorical concepts of species

Luckow (1995) has recently recognized that species categories fall into two well-defined categories: those based on causal theories and mechanisms (mechanistic concepts), and those based on history (historical concepts). The former view species as units that undergo evolution; the latter as end products of evolution. Despite their apparently slight distinction, the two views reflect radically different ways of looking at the problem, and express a philosophical split between historical and ahistorical approaches to biological phenomena. Ahistorical or mechanistic concepts of species normally rely on proximal, population-based, phenomena and are rooted in microevolutionary traditions of population genetics and ecology. They include the biological species concept (Mayr, 1942, 1963), ecological species concept (Van Valen, 1976), species mate recognition system (Paterson, 1985), cohesion concept (Templeton, 1989), and many others. These various ahistorical views of species contrast markedly with the strongly history-based foundations of modern systematics, and led some to consider that definitions of species belong elsewhere: “the species concept, which is a theoretical idea, does not belong to systematics or taxonomy [...] and never has” (Szalay and Book, 1991: 10).

As noted before (Kluge, 1990; Luckow, 1995), most mechanistic concepts rely on assumptions about the process of speciation, with species as sole participants in the process. An obvious flaw in such an approach is that the process that gave rise to an entity cannot be understood before the entity itself is defined (Rieppel, 1986). Thus, basing species concepts on models of speciation results in a logical inconsistency. Some do not see that situation as necessarily undesirable. Mishler and Brandon (1987), for example, argue that there can be a single optimal classification, but the optimal criterion for recognizing species may be different in different groups. Thus, one could recog-

nize species based on the causal process considered most important in generating and maintaining lineages in a particular group. Such arguments, however, imply that species are uncomparable units in the living world, and that any agreement on the delimitation of a species is coincidental and therefore of limited biological significance (Luckow, 1995). One is reminded here of the main arguments justifying the use of phylogenetic criteria to delimit taxa: they are the only ones general to the whole of evolving life, and therefore the best possible general system of reference. Other criteria for delimiting groups are imaginable, as has been done in evolutionary taxonomy to define grades. The generality of such criteria, however, is restricted to the elements used to define them, and their predictive power is limited or nonexistent. The motivation that justified the search for a general notion of monophyly in the past also propels the search for a general concept of species. And just as with monophyletic groups, the way to proceed with that search is to trace the path of history, i.e. phylogenetic patterns. In this sense, I oppose pluralistic views of species (Mishler and Donoghue, 1982; Kitcher, 1984; Mishler and Brandon, 1987; De Queiroz and Donoghue, 1988; Ereshefsky, 1992; Baum and Shaw, 1995), according to which species may be individuated by various kinds of connections, and different definitions may all be correct according to context. I advocate that, inasmuch as the species concept is considered to belong to systematics, there are universal guidelines for recognizing species taxa as comparable units in any group of organisms.

Historical concepts of species

Generally speaking, historical concepts view species as end products of evolution. They are based either directly on character evidence or on hypotheses about ancestry, or a combination of the two. Various species concepts and versions thereof have been made within the phylogenetic paradigm, and individual authors have on occasion defended different versions along their careers. Much confusion remains about the names these concepts bear in the literature. Several different definitions have claimed the name ‘Phylogenetic species concept’, obviously because of the current appeal of the word ‘phylogenetic’. Here I use that name only for the concept associated with its first recognized usage, by Cracraft (1983). Because of terminological uncertainty, the names used below

should not be taken to imply uniform usage in the literature. Despite the multiplicity of opinions, phylogenetic species concepts can all be grouped into two broad points of view. In one, which I call lineage-based, species rely on inferences about lineage structure, ancestor-descendant relationships or tokogenetic relationships. The second group of concepts, here called pattern-based, consider species real only to the extent that they rely on direct character evidence. Below I provide a brief description and discussion of each tendency and enumerate its main proponents and critics.

Lineage-based concepts

Hennigian species concept

This was originally proposed by Hennig (1966) and later endorsed by few authors, including Brundin (1972) and Ridley (1989). Hennig's elaborate notion of species was based on reproductive communities and genetic discontinuity and, in those aspects, was rather close to the biological species concept. For Hennig, species form by the split of a reproductive community into two mutually isolated communities of reproduction. He considered that, when such a splitting even occurs, there is always a change of at least one character of the ancestral species in at least one of the daughter species. Hennig did not require change of both daughter species to recognize them as separate species, allowing that one of them might be identical to the ancestral species. As a consequence, he did not expect species to be monophyletic or to necessarily be diagnosable by autapomorphies. On a cladogram, a Hennigian species is represented by the part of a phylogeny between two cladogenetic events, i.e. the line between any two nodes. This last point, which was proposed as a methodological tool for estimating the duration of species in a continuum, gave rise to the once widespread criticism that, for cladism, ancestral species go extinct when there is a speciation event. The main problem with the Hennigian concept is that it has little empirical bearing on how species are delimited in practice so as to serve as units for phylogenetic analysis, a problem of which Hennig himself was aware. Although Hennig's ideas on species provided a firm basis on which to better understand the phylogenetic meaning of the biological species concept, it went little beyond it in empirical content.

Evolutionary species concept

Originally proposed by Simpson (1961), and later modified by Wiley (1978, 1981), it states that "a species is 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, 1978: 18). This concept has been relatively well accepted, at least compared with other concepts in the phylogenetic era. Its most obvious points of contention are its resort to "evolutionary tendencies" and "historical fate". These are prospective narrative predications (O'Hara, 1993; notice that the author did not consider this to be a deficiency), i.e. statements that depend on future outcome. The truth or falsehood of prospective narrative sentences depends on future events, and is logically indeterminable in the present. These elements make the evolutionary species concept perhaps the most self-consistent of the lineage-based concepts. However, these very same characteristics rob this concept of its empirical content, and led some to consider it as "highly non-operational" (Panchen, 1992: 338). Earlier, Rosen (1978: 176) also objected to the element of subjectivity of this concept, and stated that "the evolutionary species appears to conform, in practice, with Regan's (1926) definition that a species is what a competent taxonomist says it is". Rosen, however, did not cite any specific authors for his version of the evolutionary species concept.

Genealogical species concept

This concept appeared as a modification of the monophyletic species concept (see below) and some authors place them in the same category. I prefer to restrict the monophyletic species concept to those definitions that base species propositions on an explicit character basis, rather than on inferences about descent. The genealogical concept is presented in Baum (1992) and Baum and Shaw (1995), but some of its elements date back to De Queiroz and Donoghue (1988). It is defined as the smallest exclusive monophyletic group. The notion of exclusivity was presented as an important new concept (Baum, 1992). However, as pointed out by Luckow (1995: 593), this notion does not differ from Hennig's (1966) original definition of monophyly. It is simply an extension of the concept of monophyly to reticulate systems, where its application is notoriously problematic because of non-hierarchical inheritance of characters in biparental organisms (Nixon and Wheeler, 1990; Davis and Nixon, 1992; Davis, 1997). Originally, the proponents

of this concept focused on monophyletic sets of organisms in a reticulate system, so that the offspring of any mating pair would constitute a monophyletic group. Therefore, in a population of biparental organisms, there could be many 'monophyletic' groups with partly overlapping membership. This undesirable characteristic, at odds with the most basic logic of monophyly, led some of its supporters to shift emphasis from organismal descent relationships to character descent relationships (Baum and Shaw, 1995). Under this new approach, the incongruence between species and gene trees is circumvented by adjusting the species level to the point where there is coalescence of all known gene trees. The definition is that species are "a basal group of organisms all of whose genes coalesce more recently with each other than with those of any other organisms outside the group." One direct result is that there can be hierarchic structure within species, which are therefore not the minimal elements of phylogenetic analysis. The authors also offered a modified definition, in which species are taxa whose relationships with other taxa are primarily divergent, but whose parts (the organisms ascribed to the taxon) are related to each other by a predominantly reticulate genealogy. The ideas here comprised under the genealogical species concept have been severely criticized by Davis (1997).

Pattern-based concepts

Monophyletic species concept

This concept requires species to be monophyletic groups, just like any other taxa. In contrast to the genealogical species concept above, this concept offers a window for empirical, character-based, taxonomic action. Species would be the least-inclusive monophyletic units detectable by analysis. Therefore, only species diagnosable by autapomorphies can be accepted as valid. This concept was defended by Rosen (1978, 1979) and Donoghue (1985). The obvious practical drawback of this notion is what to do with 'species' recognized and readily diagnosable by a combination of characteristics yet lacking autapomorphies. One proposal (Donoghue, 1985) is that they be called metasppecies and not be given formal taxonomic status, an idea subsequently expanded to that of metataxon (Archibald, 1994).

Phylogenetic species concept

This concept was originally referred to by this name in Cracraft (1983), which is a version of the concept

proposed earlier by a number of authors in the early 1980s. The versions are similar: "a species is a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind" (Eldredge and Cracraft, 1980: 92); "species are ... the smallest detected samples of self-perpetuating organisms that have unique sets of characters" (Nelson and Platnick, 1981: 11–12); "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft, 1983: 170) or "an irreducible cluster of organisms, within which there is a parental pattern of ancestry and descent, and which is diagnosably distinct from other such clusters" (Cracraft, 1987). In all these versions, the notion of 'ancestry and descent' refers to the idea of self-perpetuation, or life cycle, as will be explored later in this paper. Most authors (e.g. Luckow, 1995; Davis, 1997) place these concepts along with those in the next category, within an expanded 'phylogenetic species concept'. However, the original concepts of Eldredge and Cracraft (1980), Nelson and Platnick (1981) and Cracraft (1983) differ considerably from more recent versions treated under the same name, in that they rely exclusively on character differentiation and diagnosability, rather than on notions of lineages or populations. Despite the terminology, none of the species concepts in this category actually rely on phylogenetic concepts. A hypothesis of relationships expressed as a branching diagram would have no bearing on the limits and composition of individual species taxa.

Neophylogenetic species concept

This term is coined to accommodate the proposals of Nixon and Wheeler (1990, 1992) and Davis and Nixon (1992), formerly called 'Phylogenetic species concept'. Species are defined as "the smallest aggregations of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon and Wheeler, 1990: 218). As with the previous category, this one does not rely on any phylogenetic concepts, and any information derived from phylogenetic hypotheses is therefore irrelevant to the recognition of species taxa. This concept is a close conceptual relative of the previous one, but differs in requiring the notion of lineages and populations. That distinction is relevant for the purposes of this paper,

because of the bridge that will subsequently be made between the previous concept and the next.

Individual organism species concept

This is not properly a species concept, but rather a denial of the relevance of species concepts to phylogenetic reconstruction, or at least of the way the discussion has been conducted in the literature. It was most emphatically defended by Vrana and Wheeler (1992), with previous support by Donoghue (1985) and some of the notions included under the phylogenetic species concept. It argues that individual organisms are the terminal entities used as data sources for phylogenetic analysis. Based on these, hypotheses of monophyly are formulated. There is no need for clusters of individual organisms of doubtful monophyly, and reproductive ties are irrelevant for reconstructing relationships. The argument developed by Vrana and Wheeler relies on the ideas of Nelson (1989a, b) about lack of empirical difference between species and other taxa (see below). This concept has been negatively received by most authors, probably because its basics are in tune with the pattern cladistic view of systematics. Most criticism is rather vague, however, and laments the fact that this concept downplays and runs over issues of relevance to population biology. O'Hara (1992: 243), for example, criticized use of individual organisms as terminal taxa on two bases: first, that this solution evades the question of species delimitation entirely; and second, that it requires recovering a reticulate sequence of events. The first objection misses the point of the proposal, because the idea of species as individual organisms is a proposal about strategy for work, more than it is about the ontology of species. By treating terminal entities as individual organisms in a phylogenetic analysis, it is possible to recover patterns that in turn may shed light on the nature of species, if such an entity exists. O'Hara's opposition is puzzling, since the author himself recommends that systematists get over the species problem and carry on with their work. O'Hara's second objection seems to rely on misunderstanding, because the objective of conducting cladistic analysis is exactly to reveal hierarchical pattern, where it exists. And the only way to know that it exists is to search for it. Reticulate relationships will show up as unresolved leftovers, with either individual organisms or clusters to them as terminals. Similar criticisms were made by Frost and Kluge (1994), who consider that the approach by Vrana and Wheeler is the use

of operationalism to evade the issue of species as a reconciliation between phylogeny and tokogeny.

Elements of the problem

Rather than to separately analyse the various definitions above, I choose to discuss the main conceptual elements that enter into their notions of species. These elements are common to several of the definitions and an adequate understanding of them contributes to clarify the relative merits and drawbacks of each species concept.

Species and monophyly

The notion of monophyly in a strict sense (i.e. Hennigian) is today unanimously accepted as a general principle for recognition of groups. Although there is no controversy regarding the application of monophyly to supraspecific taxa, the same is not true at the species level. General acceptance of cladistics as a paradigm in systematics has revealed a tension between monophyly and interbreeding as the central factor in defining species (Rosen, 1978, 1979; Bremer and Wanntorp, 1979; De Queiroz and Donoghue, 1988). The two notions do not always agree, and self-perpetuating communities do not necessarily constitute demonstrably monophyletic groups. For biparental organisms, ability to interbreed has been recognized for a long time as a plesiomorphic feature, and this to be invalid as evidence of exclusive common ancestry (Rosen, 1978). There are also cases in which grouping by ability to interbreed has actually led to the recognition of demonstrably paraphyletic groups (Bremer and Wanntorp, 1979). Because monophyletic groups are the only ones that are historically meaningful, the tension between interbreeding and monophyly reflects the tension between historical and ahistorical approaches to biology, or, as Nelson (1989a: 288) more specifically puts it, between a "model (of biological species, of 'population thinking' [...]) and the results of a discovery procedure (cladistics)." Curiously, in the tradition of evolutionary taxonomy and the 'modern synthesis', species were seen as real entities, while supra-specific taxa were considered as arbitrary and subjective (Simpson, 1961; Mayr, 1963, 1969). Today, with a widely accepted and objective concept of monophyly, the situation is the reverse, with monophyletic groups considered as objective and 'real' representations of phylogenetic history and the species as a fuzzy

and poorly defined intermediate between individual organisms and monophyletic groups.

A central question today is therefore whether species should be legitimized on the same basis as other groups, i.e. by demonstration of their monophyly. To understand the discussion in all its ramifications, it is necessary to have a clear definition of the meaning of monophyly. The currently prevailing idea of monophyly dates back to Hennig (1966), who defined it in two different ways: (1) a group of species descended from a single stem species and which includes all species descended from it; and (2) a group of species in which every species is more closely related to every other species in the group than to any other species outside it. Clearly, the first definition emphasizes common ancestry, while the second relies on exclusivity of kinship. The difference between the two was not relevant to Hennig, because he was explicitly dealing with groups of species, or more precisely, with predominantly hierarchic descent systems. In such cases, the two definitions are synonymous for all practical purposes. However, as has been noticed by others (De Queiroz and Donoghue, 1990; Davis, 1997), the difference becomes relevant when we consider species and population levels in sexual organisms, and when descent systems become increasingly reticulate. Davis (1997: 378–381) argued that under reticulate systems the first of Hennig's definitions of monophyly still applies, though without the implication of nesting or exclusivity that it has in strictly hierarchic systems. The second definition, however, is meaningless in a non-hierarchic framework. In any case, however, it seems that the idea of monophyly in reticulate systems stands uncomfortably out of context, and applying it in those cases is stretching the concept beyond its tolerable limits and is of doubtful usefulness.

Be that as it may, the history of species concepts based on monophyly is rather convoluted. Apparently the first explicit suggestions of monophyletic species concepts were by Rosen (1978, 1979), followed by Mishler and Donoghue (1982), Donoghue (1985) and Mishler (1985). The argument was that phylogenetic systematics requires groups to be monophyletic, and that species should not be exceptions to that rule. Donoghue (1985) proposed species to be the smallest monophyletic groups of organisms, with individual organisms used as terminals in phylogenetic analysis (in that regard, an opinion rather close to the subsequent suggestion of Vrana and Wheeler, 1992). Results of the analysis would

then cluster some individuals on the basis of their apomorphic characters. The smallest such clusters should be considered species. Leftover clumps of individuals lacking apomorphies for membership in other groups yet also lacking apomorphies of their own were called metasppecies and, not being demonstrably monophyletic, did not warrant formal taxonomic recognition. Such early proposals for monophyletic species were self-consistent and little theoretical criticism can be raised against them except, perhaps, that an immense proportion of known species would probably have to be demoted to metasppecies. It is questionable whether a concept that excludes such a large portion of known diversity is useful or biologically meaningful.

Later, the requirement of monophyly for species was gradually loosened, as problems with the concept in non-hierarchic systems surfaced and, perhaps mistakenly, were considered important. De Queiroz and Donoghue (1988), for example, maintained a requirement of monophyly for species, but considered it inappropriate to inquire about phylogenetic relationships among interbreeding organisms, because of their non-nested pattern of relationships. The authors thus pushed the problem one level down, and concluded that populations were the actual 'basal units' of phylogenetic analysis. Populations were defined as sets of organisms within which relationships were reticulate, and between which relationships were predominantly diverging. Davis (1997: 381–382) pointed out a number of problems with De Queiroz and Donoghue's requirement that all taxa be monophyletic and their concomitant waiver of that requirement for populations, the basal units of analysis. Indeed, De Queiroz and Donoghue conceded that an individual population can be monophyletic but failed to provide an explanation of how that could be determined, and why such a population would not be simply a species.

The notion of monophyly has been gradually modified by more recent proponents of monophyletic species concepts, to allow its application to reticulate descent systems. However, the ramifications of the notion of monophyly in such cases are so complex and multifarious that one wonders whether the concept should retain that name. Also, and more importantly, the impact of such controversy for practical action on species recognition seems to have been nil.

Application of the notion of monophyly to single species has been considered inappropriate by some authors (Platnick, 1977; Ax, 1987; Davis and Nixon, 1992; Davis, 1997), because "if phylogenetic species

are the minimal elements of phylogenetics, they cannot themselves be monophyletic groupings of lesser units; rather, the minimal *monophyletic group* is a set of two or more of these minimal *phylogenetic elements*" and "if phylogenetic species are the minimal hierarchically related elements of phylogenetic systems, it follows that an individual phylogenetic species cannot be resolved as a monophyletic grouping by conducting a phylogenetic analysis of lesser elements" (Davis, 1997: 376; italics original). I would call attention, however, to a few problems with that idea. First, species, in whatever form, consist of individual organisms, themselves the units upon which observations are ultimately made (De Queiroz and Donoghue, 1988: 319). Species can only be considered as minimal elements of phylogenetic relationship, not the minimal elements of analysis. One can certainly include several terminals representing the same species in a phylogenetic analysis, and that will not result in any theoretical or practical problem. Second, it is not necessary to resolve relationships within a group to demonstrate its monophyly; all one need do is to include a certain number of putative members of the group in the analysis. If they all come out as monophyletic, then the hypothesis is corroborated, regardless of their intrarelations being unresolved, if that is the case. Third, the limit of species is not something that is determined by means independent of phylogenetic hypothesis. There can be mistakes in delimiting species compositions, and such mistakes can be located and corrected by considering the possibility that a given species is a complex assemblage (i.e. para- or polyphyletic). Considering species as immune to phylogenetic qualification presupposes a means of delimiting them that is above and beyond systematic method, which is obviously not the case. I find it somewhat puzzling that Davis and Nixon (1992) and Davis (1997) consider phylogenetic species as indivisible, when in Davis and Nixon (1992: 430–432) it is conceded that they can sometimes be subdivided into populations. On another point, a species which is the sister group to two or more others, and is itself diagnosable by autapomorphies and is not divisible into subunits, is clearly a monophyletic group. The autapomorphies indicate that the species has a history independent of that of others around it, and its closest relatives have simply gone extinct without a trace.

Consider, for example, a biological entity such as the recent bowfin, *Amia calva*. It forms an extant pool of self-perpetuating fishes currently inhabiting

swampy areas in the south-eastern United States. The species is the only extant representative of the family Amiidae, order Amiiiformes, and subdivision Halecomorphi (sister group to Teleostei, with some 20 000 Recent species). Compared with teleosts, *A. calva* has a large set of autapomorphies indicating that it has had a long history independent of that of its sister group. When fossils are included in the picture (as was done by Grande and Bemis, 1998), several of these apparent 'autapomorphies' become synapomorphies for members of groups composed of *A. calva* plus various of its extinct relatives. Obviously, characters apomorphic for *A. calva*, when compared to other actinopterygians, indicate monophyly. Monophyly of several internested groups, as it turns out, but still indicative of monophyly. If the fossil relatives of *A. calva* were unknown, all we would have would be its autapomorphies. There is nothing to gain by ignoring the fact that *A. calva* represents a monophyletic group, although today with only a single 'species'. If species are defined as the smallest units of hierarchical structure, then clearly that is the last level where the concept of monophyly still applies. Therefore, if a species is diagnosed by one or more autapomorphies, it should consistently be considered a monophyletic group.

Tokogeny and phylogeny

Reproduction in biparental organisms involves two separate somatic forms, adult males and females. Because there can be genetic recombination in each generation, the pattern of descent among individual organisms is reticulate. Descent systems in which reticulation predominates are called tokogenetic, and are considered to be the rule within species or populations of sexually reproducing organisms. In tokogenetic systems, characters are not normally segregated in lineages and do not tend to form internested patterns of similarity. Therefore, reconstruction of tokogenetic relationships is difficult or impossible for most categories of characters. Phylogeny, in contrast, is characterized by descent systems in which relationships are predominantly divergent, with little or no exchange of genetic information among constituent elements. Because there is strong character segregation in phylogenetic systems, characters tend to be arranged hierarchically, in internested sets of more or less inclusive similarity. Reconstructing the pattern of descent in phylogenetic systems is thus possible by backreading characteristics observable in individual

organisms. In the abstract model, phylogeny starts where tokogeny ends and vice versa, but in reality the separation is not clear cut. There are cases of reticulation in predominantly hierarchic systems and cases of hierarchical character segregation in predominantly reticulate systems. Obviously, the difference between phylogeny and tokogeny is meaningful only for biparental organisms. Relationships are always hierarchical in asexual descent systems.

Tokogeny is also related to the question of cohesion, i.e. that there is some kind of force or factor keeping the various elements of a species together (or “sticking together”; De Queiroz and Donoghue, 1988). Reproductive ties are traditionally considered the cohesive force in species composed of sexually reproducing organisms (Wiley, 1981). For some, sexual cohesion is deemed so important that strictly asexual organisms are considered not to form species or entities of a level higher than organism lineages (Hull, 1980). One wonders, then, how several groups of uniparental organisms have patterns of relationships (groups within groups) as well-defined by characters as in sexual groups. Action of constraint, inertia, or stasis have been claimed as explanations, but fail insofar as they may account for similarity among individuals within a ‘species’, but not for hierarchic patterns of character distributions among them.

The separation between phylogeny and tokogeny is normally considered to be of critical importance in understanding the relationship between evolution and phylogeny. Because species are considered to be active players in the evolutionary arena and the ultimate makers of phylogeny, the issue is therefore relevant to the species problem. Hennig (1966) concluded that the species level should be recognized at the interface between tokogeny and phylogeny. More precisely, he suggested that the interface would be an appropriate level at which to recognize the entity normally called species. Clearly, the species in this scenario has a special importance as the connection between the mechanistic arena of reproduction and self-perpetuation and the world of frozen phylogenetic relationships, or history. The attractiveness of this model resulted in the proposal of many species concepts based on sexual reproduction, which obviously apply only to biparental organisms. Most famous among these is the biological species concept (Mayr, 1942, 1963), prevalent throughout the period of the modern synthesis.

Species definitions based on the phylogeny/tokogeny interface apply only to a subset of living

beings, and are not of general biological significance. As argued by Vrana and Wheeler (1992), the emphasis of species definitions on sexual (biparental) lineages is such a tremendous theoretical and practical drawback that one is led to question whether such definitions deserve the high profile they have in biology. The emphasis on species concepts applying only to multicellular, sexually reproducing organisms presumes that asexual organisms are “an insignificant minority unworthy of consideration in a general theory of biology” (Vrana and Wheeler, 1992: 70). However, “each of the sexual species hosts at least several of the asexual – protozoan, fungal, bacterial and viral – then it must be the former that seem insignificant and aberrant in general biological mechanisms” (Vrana and Wheeler, 1992: 70). Clearly, species concepts restricted to biparental organisms are either admittedly limited or based on ignorance of biological diversity.

Mechanisms of genetic exchange are known in prokaryotes, but seem not to constrain divergence between populations, and if so, sexual isolation may not be a prerequisite for evolutionary divergence in prokaryotes (Cohan, 1994). In addition, genetic interchange in prokaryotes is far more ‘promiscuous’ than in eukaryotes. Bacteria may undergo homologous recombination with organisms markedly divergent in DNA sequence (Roberts and Cohan, 1993), and plasmids can transfer gene operons across widely divergent taxa – even between members of different phyla (Flavell, 1992). Thus, if the term ‘sexual reproduction’ is to be applied to prokaryotes, it certainly refers to something quite distinct from the phenomenon normally covered by that name in eukaryotes.

At any rate, it seems clear that sexual reproduction is not a property well defined or widespread enough to serve as a general parameter. It is rather a synapomorphy for a subclade of living organisms. Therefore, the derivative notion of an interface between tokogeny and phylogeny cannot constitute a consistent principle on which to base generally applicable species concepts. A general property of living beings is descent, not sexual reproduction and even descent has to be understood in context, because fossil taxa are as much representatives of living diversity as extant organisms, and within the latter, sterile individuals are no less living than their fertile relatives.

On methodological grounds, defenders of the idea that the species is an actual, or at any rate desirable, cutoff separating tokogeny and phylogeny are necessarily also defending the idea of a limit to hierarchic pattern discovery. This idea necessarily relies on the

assumption that we already know the limit of resolution of phylogenetic relationships, i.e. the ontological limit of systematics. Evidence is clear, however, that hierarchic organization often exists and is recoverable below the level of what has been called a 'species' or 'population' (Bowen and Grant, 1997; Strange and Burr, 1997; Gleason et al., 1998). Subunits of interbreeding species can be, and now routinely are, diagnosed on the basis of high-resolution assays (Avice, 1994). Also, as emphasized by Luckow (1995), the popular notion that lack of resolution necessarily indicates reticulate structure of descent is false. Lack of resolution can derive from several causes, none of which can be unambiguously tied to reticulation. Thus, the limit between tokogeny and phylogeny is by no means clearly defined by systematic methodology.

Taxa and the unit of evolution

Part of the species controversy revolves around the idea of a unit of evolution, or the notion that there is a level of biological organization that is the platform where evolutionary action takes place, or the relevant part of it anyway. For many traditional taxonomists, that unit is the species, which is presumed to evolve as a unified entity, wherein genetic information is in a certain way free-flowing (or a "field for gene recombination"; Carson, 1957) in biparental organisms.

Others see it differently. Because species can have local variations, the populations, or demes, are the basic units of evolution (Bunge, 1981). Others still prefer to scale down one more step, and the unit of evolution is the individual organism, which is the player that actually interacts with other organisms and the environment, lives, dies and leaves more or fewer offspring. Many researchers at the molecular level, in turn, see the unit of evolution as the genome, or the gene, or parts of genes, or codons, or DNA sites, since these are the bits and pieces of information that actually change in kind or frequency from generation to generation and in turn determine all other scales of observable change. Clearly, the individual organism is by no means a unified entity when it comes to evolutionary processes. Maternally inherited traits, such as mitochondrial or chloroplast genes, evolve independently of the organism that carries them. Patterns of relationships derived from that kind of data will reflect the phylogeny of mitochondrial or chloroplast types and not necessarily the pattern of relationships among the organisms with which they are associated

(Doyle, 1992). Considering current knowledge, mitochondria and chloroplasts might as well be considered as separate taxa, with their own taxonomies.

The question of the unit of evolution relates to scaling, which, under a reductionist agenda, results in an infinite regression, with the 'unit' at each level revealing patterns relevant for a particular set of phenomena. Naturally, specialists at each level claim the privilege of dealing directly with the basic unit, a common theme in the history of the sciences. Perhaps the only way to accept the idea of a unit of evolution is to side with pragmatism, and to consider the problem of unit as meaningful only within a specific phenomenological stratum, with its particular focal level. Therefore, the question of the unit of evolution is insoluble as a general question, and empty as a conceptual issue. Resolution of phylogenetic relationships is itself not subject to an absolute lower bound. It is possible to resolve relationships within what is normally called an interbreeding population, if data displaying relevant variation are available (e.g. Avice et al., 1987).

Now, must the notion of species necessarily rely on the idea of a unit of evolution? In the same way that the fact that genes evolve does not preclude the fact that individuals evolve, the fact that 'species', in whatever guise, evolve does not preclude the fact that higher taxa evolve. The idea that species evolve while higher taxa do not relies on a restrictive view of the nature of taxa and of what constitutes evolution. The evolution of individual genes produces larger-scale effects in the individual that carries them, which in turn interacts with other individuals to result in observable effects in the population of which they are part. The process goes on in a continuum, to generate 'species' and higher taxa, which are themselves composed of evolving units and therefore evolve as well. Obviously, the interactions at each level, as well as their results, are different, and the taxon *Vertebrata* evolves in a different way from the species *Silurus glanis*, which evolves differently still from its mitochondrial genes. Yet, no specific level has the primacy of carrying the 'real' evolving units, though some have unduly attained that status.

Nelson (1989a) proposed that taxa should be seen as relationships, rather than as groups of organisms. If so, taxa are inherited along with homologies, from organisms that are connected by descent. Taxa therefore are properties of organisms. The discovery procedure of cladistics reveals taxa on the basis of homologies, or synapomorphies. Now, did the taxon

Teleostei begin its existence with the first teleost, and then continue to exist to the present? If so, did other teleostean subtaxa come into being in the meantime, along with their respective taxa? These questions are impossible to answer, insofar as all we know is that there is a taxon indicating a relationship between several recent and fossil organisms, which we call Teleostei. The relationship between such organisms is inferred by shared homologies, nothing else.

Speculating about the first teleost and its characteristics is an empty exercise in nominalism, with no bearing on the actual meaning of taxa in biology. Homologies allowing us to recognize Teleostei as a taxon did not necessarily come into existence along with the taxon as we recognize it. The reasons for this are two. The first one is trivial, and stems from the fact that extinction telescopes character to branches between surviving lineages (more precisely, between lineages surviving to our knowledge) (Nixon and Wheeler, 1992: 136–137).

For example, consider the scheme shown in Figure 1A with terminal taxa A–J and synapomorphies represented by black rectangles. Consider now that taxa C, D, E, G and H, represented by broken lines in Figure 1B, are unknown. The fact that unknown groups are what they are, unknown, makes synapomorphies for clades (ABC) and (ABCD) concentrate as synapomorphies for the clade (AB), for all practical purposes. The same happens for the synapomorphies for (GHIJ) and (HIJ), which telescope to clade (IJ) only. The result is as shown in Figure 1C, with character corroboration for clades (AB) and (IJ) four and two times, respectively, as strong as they would otherwise be. The homologies that indicate taxon (AB), thus, cannot be interpreted literally, i.e. as having a history fully coordinated with that of the recognized taxon. The empirical evidence for clade (AB) is in fact evidence for various taxa in which A and B participate, which we know nothing about.

While that may be seen by some as a misrepresentation of actual history, it is not so if the meaning of taxa and their supporting characters is properly understood. Corroboration for interested taxa is cumulative, and all they provide is empirical support for the taxon, not a blueprint of its evolution. This point was made in passing by Nelson (1989a: 285), but subsequently misinterpreted by De Queiroz and Donoghue (1990: 66), who contended that “it is logically impossible for a taxon to acquire apomorphies after its earliest representatives have lived and died.” Obviously, De Queiroz and Donoghue

rely on a model about the evolution of taxa which is widespread, yet unrealistic relative to the actual methods available for pattern reconstruction. Few would believe that all apomorphies for Mammalia, for example, appeared all at once with the ‘first’ mammal. The currently recognized set of mammalian synapomorphies most likely accumulated across several successive lineages, many of which disappeared without trace. So, the perception we have of a taxon may have little to do with its origin, and the elements we have as evidence for its existence (i.e. synapomorphies) may have come into being at levels we do not suspect. That does not mean that our perception of taxa has little to do with their history. The origin of a taxon is only a small part of its history and that of its characters. Phylogenetic analysis permits us to make several inferences about a taxon’s history, but its origin is not among them. The origin of taxa, if at all a concrete notion to pursue, lies beyond the empirical horizon of systematics. As Nelson (1987d: xii) noted: “Were [evolutionists] entirely wise rather than adversarial they would never claim to have done the impossible: to have proved the correctness of their views by offering evidence of origins of things [...] A point – an origin – is where the evidence [...] disappears.”

The second reason why homologies of a taxon are not necessarily coordinated with its ‘origin’ is directly related to character transitions. To understand this, we must first comprehend some aspects of the dynamics of homoplasy. Synapomorphies perceived as evidence for a taxon are supposed to be homologies, or character transitions, inherited from its exclusive common ancestor. Homoplasy is normally seen as empirical evidence that disagrees with the hypothesized pattern, either totally or partially. However, homoplasy, being random in principle, will occur not only in disagreement with the pattern – the version of homoplasy we normally care about – but also in agreement with it. Homoplasy that agrees with the pattern will not be recognized as such.

In Figure 2, we have ‘real’ synapomorphies 1 and 2 for taxon (DE), but also a homoplasy, character 3, occurring in sister taxa D and E. Character 3 will not be recognized as homoplastic, and for all purposes will be one more element among the set of homologies supporting taxon DE. This reasoning was used by Farris (1983) to explain why parsimony analysis will not be misleading in the face of abundant homoplasy, and also proves useful to demonstrate that the relationship between characters and taxa is

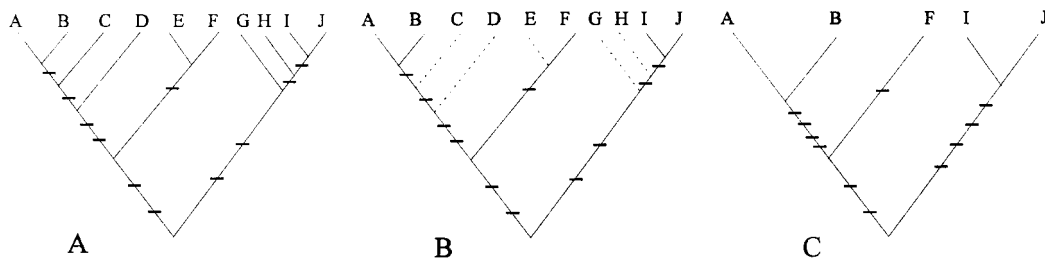


Figure 1. Phylogeny of taxa A-J. In diagram A, all terminals are included; in diagram B, taxa C, D, E, G and H, shown in broken lines, are unknown and therefore not included in the analysis. The truncated phylogeny of taxa A, B, F, I and J diagram C, shows 'telescoped' support for groups (AB) and (IJ). Black rectangles represent synapomorphies.

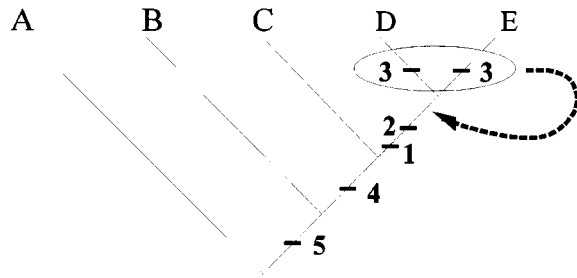


Figure 2. Hidden homoplasy. Character 3 is convergent in taxa D and E, but because the two are sister groups on the basis of other characters, character 3 is interpreted as synapomorphic rather than homoplastic.

not literal. Homologies do not necessarily come into being along with their respective taxa. An unspecified proportion of homologies for a taxon are always illusory. Illusory yet not misleading, since the clade they specify is monophyletic according to available evidence. Now, if real and illusory homologies cannot be distinguished, then what if all synapomorphies are homoplastic in this sense? Would this mean that they do not constitute evidence of relationship? Definitely not. It would mean that a model of descent with modification, as normally understood, is not a valid explanation for hierarchic patterns of similarity. If 'illusory' homologies have to be reckoned as evidence then it really doesn't matter if characters have unique origins after all.

The points raised above show that the idea that species evolve and higher taxa do not is simplistic, and relies on an unrealistic view of the ontological relationship between characters and taxa. In reality, the continuous process of descent visibly operating at the terminal tips of cladograms does have a dynamic impact on our perception of taxa. Perhaps this effect becomes gradually less important as we move down the cladogram away from the tips, but no one knows

where, and if, it can be ruled out completely. If it occurs for recently differentiated taxa, then the same factors were equally important for deeper components of relationships, when they were not yet as deep. Regardless of the problems of scaling, forces acting at the tips, extinction and character change, may alter our perception of underlying taxa and their corresponding homologies. Whether the effects represent errors of some sort is a matter of interpretation, and depends on how much one wishes to believe in a pattern independent of our abilities to perceive it. A dynamic view of 'higher' taxa is certainly at odds with the usual view of clades as frozen remnants of descent with modification. Still, patterns of homologies observed in organisms are our empirical support for taxa, and frame the only window we have through which to behold them. An absolute fixist view of taxa is neither a logical conclusion from cladistic methodology that links homology and taxa, nor from a model of descent with modification. It is rather an interpretation fettered to a traditional view of the relationship between groups and the evolutionary process, one that should be abandoned for the benefit of both systematics and evolutionary theory.

Pattern and process

Long-standing, opposing views on the roles of pattern and process in comparative biology have their present-day representation in the dichotomy between 'pattern cladistics' and 'evolutionary phylogenetics' or 'phylogenetic systematics'. Modern discussion of this issue started in the 1980s, when some theoretical systematics realized that the study of evolutionary patterns would benefit if conducted independently of theories about evolutionary process. In their view, the recognition of patterns of relationships among living organisms is an investigation to be conducted without the constraint of specific evolutionary assumptions.

Patterns of diversity, rather than relying on evolutionary models, provide the basis upon which such models should be developed. Therefore, the existence of a vigorous and independent theory of pattern reconstruction would be beneficial for both systematics and evolutionary biology.

The pattern cladistics point of view has been one of the most misrepresented topics in the modern systematics literature, and is often construed as associated with anti-evolutionism and theory-free science. Such accusations are false, and are based on versions of pattern cladistics built up by its antagonists, rather than on the actual ideas of its proponents (de Latorre, 1991). That such misrepresentation persists to the present, despite the clear explanations available, is remarkable. It is pointless to repeat all the arguments here, and the reader is referred to the primary sources on pattern cladistics (Platnick, 1979, 1986; Brady, 1982, 1983, 1985; Nelson, 1985b, 1989a; Brower, in press). It is important to recognize that the pattern-versus-process controversy is simply a modern expression of an old schism between different ways of viewing comparative aspects of biology. The split extends back to at least the division between morphologists and teleologists in the 19th century.

It has been shown (Ospovat, 1978, 1981) that the dichotomy between evolutionism and creationism is not an adequate expression of the issues at stake in that period. That dichotomy was, in large measure, a result of the way arguments were posed in debates surrounding the *Origin of Species*. That was, however, just an expository device, which later became a misleading yet widespread representation of the intellectual framework of the debate. A different dichotomy, more representative of the true state of debates then, was offered by Ospovat (1978, 1981), who contrasts 19th-century teleologists with morphologists. Teleologists considered the adaptation of an organism to its environment as the single most important issue in biology. Morphologists, contrastingly, downplayed the role of adaptation, and considered "commonalities of structure as deeper indications of biological reality" (Amundson, 1998). Clearly, that dichotomy is largely equivalent to today's debate between pattern cladists and 'evolutionary phylogeneticists'.

The pattern-versus-evolution controversy is also reflected in the species problem, most strongly perceived by Baum and Donoghue (1995), who associate pattern cladistics with character-based concepts of species, and evolutionary phylogenetics with

history-based concepts. They state, "The incompatibility of history-based concepts and pattern cladistics is amply demonstrated by the fact that history-based approaches imply the existence of species that cannot be discovered by reference to characters, which is unthinkable under pattern cladistics" (Baum and Donoghue, 1995: 569). I consider this statement to be accurate. Indeed, pattern cladists, along with most other scientific enterprise, are not ready to accept hypotheses without evidence.

Supporters of history-based views, in contrast, seem to believe that there is a way to perceive history independent of characters. This is blatantly evident in all their arguments. For instance, Baum and Donoghue (1995: 570, Figure 5) offer a hypothetical example intended to demonstrate that character-based approaches can lead to historically inconsistent species limits. Their example shows four terminals, three of which are identical in all observed characters with a fourth differing in one trait. The three identical taxa, in their diagram, form a paraphyletic group. So, the argument goes, basing species definitions on characters will lead to the recognition of two 'species': one for the three identical terminals and another for the different one. Since the three identical ones do not form a monophyletic group, as their 'true' diagram shows, then character-based species concepts are potentially misleading and can lead to historically inconsistent groupings. However, one wonders that if the pattern of relationships among terminals was indeed as shown, it must have relied on some material basis, otherwise we have only two elements in the problem: two diagnosable species. If Baum and Donoghue actually believe their argument, then they certainly doubt any kind of relationship, not only at species level, and the only reliable phylogenies are those we make up. Thus, evidence simply cannot be trusted and patterns of relationships, as inferred from character evidence, mean nothing. Pattern cladists, who, unfortunately, do not have the benefit of direct observation of phylogeny, see no alternative other than relying on evidence. It must be clear that the argument against using character evidence is entirely nonsensical, and relies solely on empty speculation. Conjectures about species limits and composition simply do not exist independently of characters, and therefore rely on the same bases as all other hypotheses of relationships.

Species as individual organisms and exemplars

Discussion of the elements above suggest that the species category cannot be objectively defined as a unit of evolution, or as an interface between tokogeny and phylogeny. These concepts are either vague or immune to empirical investigation, facts that support the view that there is no conceptual difference between species and other taxa (Nelson, 1989a, b). In fact, similar opinions have been voiced for a long time, both by evolutionists and otherwise. Darwin, for instance, said "...we shall have to treat species in the same manner as those naturalists treat genera [...] we shall [...] be freed from the vain search for the undiscovered and undiscoverable essence of the term species" (Darwin, 1859: 471). In a similar vein, Agassiz, an anti-evolutionist, went as far as making pedagogical recommendations: "...the study of Species as the basis of a scientific education is a great mistake. It leads us to overrate the value of Species, and to believe that they exist in Nature in some different sense from the other groups; as if there were something more real and tangible in Species than in genera, Families, Orders, Classes, or Branches" (Agassiz, 1866: 134).

Because there seems to be no testable basis for the general recognition of species as a distinct kind of taxon on the basis of intrinsic biological properties, they should be defined as a function a phylogenetic analysis. Entities considered to be at the species level, thus, are scientifically defensible only on an operational, character-based approach. Their recognition is meaningful only to the extent that they are pieces of phylogenetic patterns. This view is hardly original, and has been defended on various occasions, e.g. "...why not cut the Gordian knot by admitting that species do not, in fact cannot exist in an evolving world, and that species are in fact what they have always been: a conceptual tool in the attempt to master biological diversity" (Rieppel, 1994: 46). Of course, species viewed as relationship can 'exist'. Even considered as a tool, species as relationship can be seen to have an objective basis, like that of other taxa.

The idea of species as an operational tool has been most radically put forward by Vrana and Wheeler (1992), who suggested that individual organisms should be the terminal entities for phylogenetic analysis, without further regard for what 'species' they might represent. Their point is that the hierarchy determined for individual organisms implies a picture

of genealogy, and the rank of species is irrelevant for that purpose. Some may be surprised to find that the idea has some precedent in Hennig's writings: "the simplest elements of systematics are the semaphoronts" (Hennig, 1966: 33) or "...the semaphoront corresponds to the individual in a certain, theoretically infinitely small, time span of its life, during which it can be considered unchangeable. In this sense *the individual is to be regarded as the lowest taxonomic group category*; it includes those semaphoronts that are connected by genetic relationships" (Hennig, 1966: 65, emphasis added). Vrana and Wheeler's proposal is fully consistent with the aims of hierarchical pattern reconstruction, and is a realistic reflection of how phylogenetic analyses are actually done. Its only limitation is that it focuses exclusively on explicit elements of a hypothesis, and overlooks the implicit generalization of taxa.

Although implicit generalizations are irrelevant for reconstruction of the genealogical pattern, they have an important role in the interaction between phylogeny, classification and other biological subdisciplines. There is general agreement that when a certain taxon, such as Teleostei, is hypothesized as monophyletic, the inclusiveness of the group extrapolates from the organisms directly examined in the course of the study. Teleostei is considered to be a taxon of more than 20 000 described species, although not more than a few tens of them have been directly examined in any single study focusing on their monophyly. The other putative teleosts are simply assumed to conform to the general pattern of relationships on the basis of subjacent evidence. This is what I call the implicit generalization of phylogenetic hypotheses, an element present in practically all systematic studies and, in fact, in all systematic traditions.

When a study demonstrates that the South American lungfish is more closely related to the cow than to the guppy or the lemon shark, the significance of the hypothesis extrapolates the particular species involved. It also extrapolates, to an even larger degree, the individual organisms that served as data sources. The hypothesis is understood as implying that lungfishes are more closely related to tetrapods than to actinopterygians or chondrichthyans.

The same argument applies to species taxa. They also have an element of implicit generalization that extrapolates the individual organisms examined, and apply to more inclusive levels of phylogenetic 'density'. Background phylogenetic knowledge permits such extrapolations to be made, which

are in fact crucial to the interpretation and use of hypotheses of relationships in a general biological context. The idea of species as individual organisms, taken strictly, lacks this element of implicit generalization, and therefore is limited in its potential to integrate with the larger body of biological knowledge. To correct that, a link must be made between individual organisms and implicit systematic generalizations. This is done by resort to the notion of exemplars, as explained below.

Phylogenetic studies dealing with large groups are often forced to reduce the number of terminals in the analysis, to fit the problem into the constraints of observational possibilities and available computational capacity. This reduction is done in two ways (Yeates, 1995). In one, called the 'groundplan method', the plesiomorphic character states for a higher taxon are inferred and the group is entered as a single terminal, hopefully representative of the character states seen in the hypothetical common ancestor of the group. The groundplan method and its reliance on 'archetypes' can be traced back to the idealistic tradition of Oken and Goethe (Rieppel, 1988). In the 'exemplar method', contrastingly, a sample of real members (i.e. individual organisms) of the higher taxon are chosen and entered as terminals in the analysis. This is the method most often used in molecular systematic studies, and it is also adopted in many morphological analyses.

The objective of both approaches is to make an analysis tractable by replacing the cladistic structure of the more inclusive group with a single terminal (in the groundplan method) or a much reduced number of terminals (in the exemplar method). This aim is best accomplished if the character states assigned to the archetypic terminal (groundplan) or the hypothetical ancestor of the reduced cladogram (exemplar) approach as much as possible the ideal result that would be expected from a complete sampling of diversity in the clade and an optimal assessment of its intrarelationships. Yeates (1995) shows that there is reason to prefer the exemplar method, on the basis of increased accuracy and transparency of assumptions. But use of both approaches can obviously lead to errors in certain circumstances, insofar as they are always a simplified picture of actual diversity. In fact, this is true even when one manages to include the whole known diversity of a clade, because unknown diversity is reasonably expected to be immense (Novacek and Wheeler, 1992). In any event, the exemplar method selects a number of

representatives (the exemplars) of a putative group which are included as separate terminals in the analysis. The relationships among the exemplars are thus resolved simultaneously with the relationships of their putative taxon to other taxa (also represented by exemplars) in the analysis. The logic behind this approach is the same as that of global analysis for ingroup and outgroup taxa (Nixon and Carpenter, 1993), which allows testing for both the monophyly and interrelationships of ingroup and outgroup simultaneously in a globally most parsimonious scheme. The choice of exemplars and their number will be a function of several factors, such as observed character diversity, availability of prior hypotheses about their interrelationships and even nomenclatural considerations (Yeates, 1995). Obviously, the greater the cladistic representation of exemplars, the more fine grained (and presumably the more accurate) will be the analysis.

The view of species as individual organisms can be combined with the underlying logic of the exemplar approach, to lend that species concept the property of implicit generalization it so far lacks. The next section examines how these general guidelines can be fruitfully implemented and combined in an operational species concept.

Species as conjectures

In the absence of an ontological basis on which to base an absolute notion of species, the only way to recognize such entities is to consider them as conjectures about integrated phylogenetic units. Species, thus, stand relative to phylogenetic analysis in a similar way as do homology statements. Homologies are conjectures about generality of attributes. They are initially based on simple similarity, and their value as evidence of relationship is interpreted literally at this point (topographical identity phase of primary homology, de Pinna, 1991; Brower and Schawaroch, 1996). Once properly coded and analysed, they can then be interpreted against a scheme of relationships. If a character maintains the same level of generality as it had when initially observed, then it is corroborated as homologous among all members of all taxa that display it. However, if the character requires more than the minimum number of steps, i.e. displays homoplasy on the preferred hypothesis, then the initial assumption of homology is refuted (in part or totally, depending on the case).

As shown in Figure 3, hypothetically based on a complete data set, the character marked with a black rectangle is homologous in taxa 1, 2, and 3 in hypothesis A, since the presence of an identical state in the three terminals is hypothesized to be the result of a single transition. In hypothesis B, contrastingly, the derived condition is not homologous between 1 and 2 on the one hand, and 3 on the other, because, in this hypothesis, the presence of the derived state in 3 cannot be explained by the same transition that explains its presence in 1 and 2. Notice that although the initial assumption of homology is refuted in hypothesis B, the refutation is only partial, because the derived state is still homologous in taxa 1 and 2.

It is today widely recognized that homology propositions can only be understood and tested against a scheme of relationships, and that homology is not an intrinsic property of attributes. Homologies are conjectures loosely based on similarity, and they can be objectively studied only by resort to specific phylogenetic hypotheses. Homologies are minimum statements about comparatively relevant similarity, subject to a process of mutual illumination including all characters in the analysis.

Before extending into further discussion about the conjectural notion of species defended here, it is necessary to resort to the notion of life cycle, as defined by Danser (1950: 118). The life cycle includes the complete history of the development of an organism and all stages of its life, i.e. the entire history of its propagation. Specimens upon which systematic research is based (i.e. Hennig's semaphoronts) are simply representations of the life cycle, and are only substitutes for the actual living beings represented by them. Danser's notion of life cycle is similar to Hennig's (1950) idea of the holomorph. The holomorph is the multidimensional totality of a semaphoront's morphological, physiological and ethological properties (Hennig, 1950: 6–8). Danser's idea of life cycle is more general than that of holomorph, insofar as it applies to taxa, rather than to a semaphoront (Nelson, 1985b: 42–43). The life cycle encompasses the idea of self-perpetuation and semaphoront, and is applicable to either sexual or asexual organisms. It also comprises the idea of characters and all their observable transformations, including replicating DNA sequences. The idea is therefore an efficient way to convey a host of subsidiary notions that must be part of a biologically meaningful species concept. Common sense holds that it would be a mistake to consider different semaphoronts, or males

and females, of the same life cycle to be different species. The life cycle is the focal point of comparative biology and the process where our perception of individual organism hinges. In a somewhat more restrictive guise, it is also recognized as fundamental to process-based theories of evolution: "Life cycles are the *sine qua non* of evolution" (Buss, 1987: 123). Therefore, the notion of life cycle conveys a host of biological concepts and properties relevant for comparative and evolutionary biology, and can be fruitfully incorporated into discussions on species concepts.

In the same way that homologies are seen as minimal units of comparable similarity, species can be seen as minimal units of phylogenetic relationships. They are initially recognized as clusters of life cycles considered to be a unit of diversity. A life cycle, in a sense, already is a cluster – of semaphoronts of the same organism. But it is a cluster that is held together by direct observation of ontogeny. Clusters of life cycles are initially just conjectures based on similarity; they can be identical for all observable characteristics or different in some traits, depending on the amount of difference estimated to be the level of phylogenetically relevant variation (i.e. intraspecific variation). At this stage, information about the descent system of the organisms can be useful, such as character-state variation in siblings or in controlled descent lineages. Representatives of the clusters thus chosen are then considered to be terminals for phylogenetic analysis. They are considered as exemplars for the taxon in question (a putative species). Depending on the results of analysis of exemplars, the initial assumptions about species limits can be corroborated or refuted to various degrees. The bearing of phylogenetic hypotheses on the initial conjectures about species limits can be directly read from a cladogram, and the guiding principle of the procedure is non-monophyly. A species-candidate assemblage of life cycles must have minimal phyletic integrity, which means that (1) its constituent members cannot be demonstrated to form a para- or polyphyletic group and (2) it must not have internal cladistic structure. If the assemblage is either monophyletic, or possibly monophyletic (without evidence of para- or polyphyly), then the conjecture that it is a species is corroborated.

Accordingly, species are here proposed as a *diagnosable sample of (observed or inferred) life cycles, represented by exemplars, hypothesized to attach to the same node in a cladogram, and which are not structured into other similarly diagnosable*

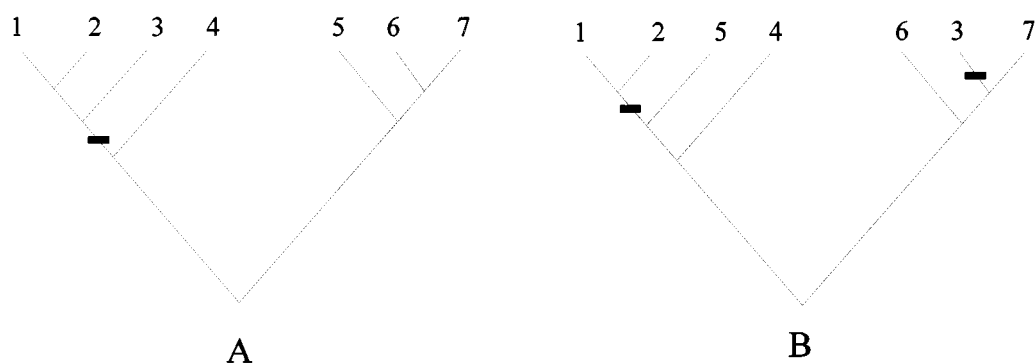


Figure 3. The character marked by the black rectangle is homologous in taxa 1, 2 and 3 in diagram A. In diagram B, the character is not homologous between 1 and 2, on the one hand, and 3 on the other. But notice that it is still homologous between 1 and 2.

clusters. This concept combines elements of several prior ideas and definitions, according to elements considered most appropriate in the discussions above. It has an explicit phylogenetic component, which permits it to be tested in a cladistic framework. The test checks their phylogenetic structuring, and can demonstrate that a given sample proposed as a species is in fact complex, i.e. more than one species. In that case the initial conjecture that the diagnosable sample is a species is refuted. The phylogenetic test of a species requires that all members of the putative species be associated with the same node in a phylogenetic diagram, and are themselves not forming a pattern of relationships. Obviously, the testing of phylogenetic integrity of the putative species only makes sense if the various representatives of it show variation for some characters. If the sample of individual organisms is monomorphic for all observable characteristics, then there is no point in further subdividing it. However, since all putative species samples display some degree of variation, the problem is to distinguish intraspecific variation from variability indicative of taxonomic differentiation. The way to test that is to subdivide the putative species into monomorphic terminals for phylogenetic analysis, which is a procedure already implemented as a tactic to minimize missing entries in data matrices (Nixon and Davis, 1991).

The way in which phylogenetic schemes can be used to test conjectures about species composition is explained in association with Figures 4 and 5. Consider a set of individual life cycles represented by individual organisms X1, X2 and X3, which are hypothesized to form a species. These three samples are included as terminals along with their putative

close relatives (unnamed terminal branches in Figures 4 and 5) in a phylogenetic analysis. Since consideration of time is irrelevant for all purposes, the schemes of relationships are represented as unrooted diagrams. Different outcomes of the phylogenetic hypothesis have different implications on the initial conjecture that X1, X2 and X3 form a species. In the hypothesis in Figure 4A, the three samples of X are associated with the same node, which corroborates that they form a species. Depending on the rooting site they can even form a monophyletic species. In Figure 4B the three terminals of putative species X also converge on the same node, but this node is not exclusive to them. In this case the hypothesis that X1, X2 and X3 form a species is also corroborated, although it will not be a monophyletic species, regardless of the rooting site. The same holds for alternative in Figure 4C. In Figure 5A, however, the initial hypothesis of phylogenetic integrity of X1, X2 and X3 is refuted, because they associate with two different nodes in the diagram. That means that one or the other cluster (represented by X1 and X2, and X3) or both will necessarily be more closely related to some terminal other than to each other. This arrangement refutes the conjecture that the three terminals composing X are conspecific, since characters are segregated in such a way as to indicate disjunct relationships for different parts of the cluster X. The same situation applies for the hypothesis in Figure 5B. In Figure 5C, the three parts of species X are associated with the same node, and in fact may form a monophyletic group if the root of the tree is located to the left of that node. Although the three subsets of X in this case have phylogenetic integrity, they also have additional cladistic structure, indicating that the cutoff to delimit the species

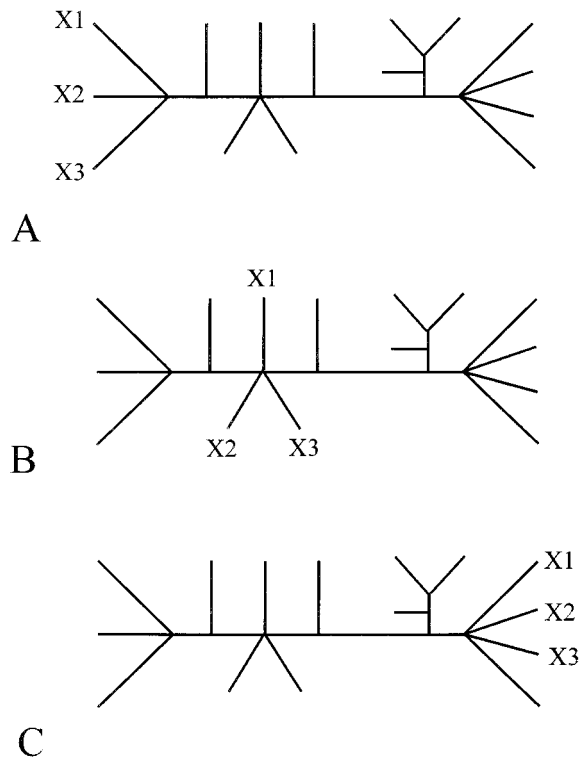


Figure 4. Some examples of possible relationships for a set of exemplars, X1, X2 and X3, hypothesized to form a species. The three exemplars are associated with a single node in A, B and C. Therefore, the phylogenetic integrity of the putative species is corroborated in all three possibilities, but only in A can the species possibly be monophyletic.

X was too coarse. The species limit in this instance would have to be decreased in inclusiveness, perhaps to include one species for X1 and X2 and another for X3. Testing this new conjecture, though, would require further subdivision of terminals and a second round of analysis.

The data required to conduct the testing suggested above should not be restricted to single characters or alleles. Even individual organisms within a sexually reproducing population can be distinguished from one another, for example with DNA fingerprinting, and that obviously will not be a reliable indication on the phyletic status of a set of exemplars. A conclusive data set will include several different character transitions (or from different loci) at the relevant nodes, so that the presence of hierarchic partition (or lack thereof) is demonstrated across a broad set of non-correlated characters.

The concept above does not require species to be demonstrably monophyletic groups, but does not

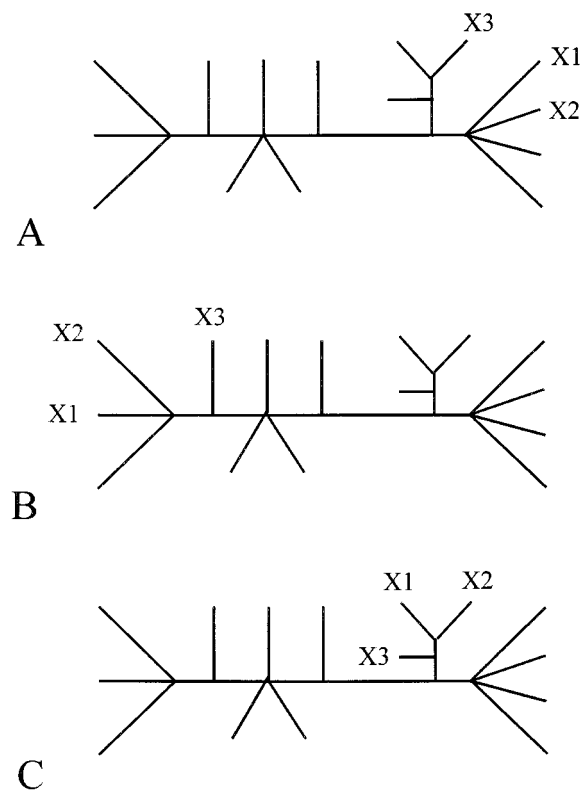


Figure 5. Cases in which the hypothesis that exemplars X1, X2 and X3 form a species is refuted. In all three cases, the three exemplars are associated with more than one node. Although hypothesis C permits that X1, X2 and X3 form a monophyletic group, the presence of additional cladistic structure indicates character segregation and consequent additional differentiation. This indicates that more than one species is involved in the problem.

allow them to be para- or polyphyletic assemblages. In fact, there is no need of a root to test a conjecture of species as proposed here. The cladistic structure in an undirected tree provides necessary and sufficient elements to check the phylogenetic integrity of a putative species. The exemplars chosen have simply to be associated with a single node, which need not be an exclusive node. Naturally, a root can be inserted to express the conclusions in more familiar terms. Demonstrably non-monophyletic clusters cannot be considered as a species. Just as with other taxa, non-monophyletic clusters have no empirical basis. Their recognition would not only be inconsistent with the basis of systematics, but also be detrimental to the study of disciplines that rely on phylogenetic patterns, such as biogeography, coevolution, and character evolution (Donoghue, 1985). I have no objection to the term metaspecies as far as it goes, but I do object that

metaspecies are less justifiable as formal taxonomic units at the species level as defined here. If the aim of the species conjecture is to delimit a minimal unit of phylogenetic integrity, then all that is necessary is that this unit not be demonstrably complex in its cladistic structure (i.e. that it is not para- or polyphyletic or monophyletic with subclades).

This conjectural view of species does not imply that the relevance of species thus recognized is restricted to elements used in their delimitation. Species in this concept are not groups of convenience in the pejorative sense, because they are elements in a chain of discovery operations. The situation is the opposite, and species recognized and acceptable under a phylogenetic framework are entities about which generalizations of several sorts can be made. They are a heuristic device to facilitate understanding of patterns of biological diversity and all their evolutionary ramifications. In the same way that monophyletic groups are the most efficient general baselines for generalizations about biological properties, so are species as recognized in a phylogenetic framework. The delimitation of species is a conjecture subject to testing, not an all-round theory, and needs to be united with other discovery operations to provide a more general picture of the meaning of patterns in evolutionary biology. In sum, species are discovered and proposed within an operationalistic agenda, and the proposal may subsequently be incorporated into more encompassing models, such as biogeography, coevolution, heterochromy, or population biology. This is similar to what now happens with monophyletic groups. They are hypothesized on the basis of character evidence only, and then put to work in other areas of biology. There are various interpretations possible of mechanistic significance of the phylogenetic integrity of a species defined according to the precepts above. Undoubtedly, sexual reproduction is an important biological property that will often be associated with species assemblages in biparental organisms. After all, reproductive isolation is a strong determinant of concordant genetic partition across loci and characters. In exclusively uniparental taxa, other factors may be associated with them, such as developmental constraints and their variations. In most living beings, we have likely a combination of different factors, all interacting in an integrated descent system.

The concept described above does not require that named species must wait for a test of phylogenetic integrity to be recognized. Just as with hypotheses of homology and taxa in a general sense, they can be

proposed on the basis of partial character evidence, and tentatively accepted as valid until their testing in an adequate context becomes possible.

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