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PHYLOGENETIC SYSTEMATICS AND THE SPECIES PROBLEM

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Abstract—A tension has arisen over the primacy of interbreeding versus monophyly in defining the species category. Manifestations of this tension include unnecessary restriction of the concept of monophyly as well as inappropriate attribution of "species" properties to "higher taxa", and vice versa. Distinctions between systems (wholes) deriving their existence from different underlying processes have been obscured by failure to acknowledge different interpretations of the concept of individuality. We identify interbreeding (resulting in populations) and evolutionary descent (resulting in monophyletic groups) as two processes of interest to phylogenetic systematists, and explore the relations between the systems resulting from these processes. In the case of sexual reproduction, populations of interbreeding organisms (regardless of whether they are monophyletic) exist as cohesive wholes and play a special role in phylogenetic systematics, being the least inclusive entities appropriate for use as terminal units in phylogenetic analysis of organismal relationships. Both sexual and asexual organisms form monophyletic groups. Accepting the reality and significance of both interbreeding and monophyly emphasizes that a conscious decision must be made regarding which phenomenon should be used to define the species category. Examination of species concepts that focus either on interbreeding or on common descent leads us to conclude that several alternatives are acceptable from the standpoint of phylogenetic systematics but that no one species concept can meet the needs of all comparative biologists.

> ". . . the task of 'ordering' (and what means the same thing, of systematics) lies in considering the unit as a member of an ordered whole. It is a fact . . . that no unit exists as a member of only one whole."
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> "Therefore it is possible to arrange animated natural things in numerous different systems, depending on which of these different relationships has been investigated. The differences among all these systems are determined by the particular relationships of which they are a concrete expression. All these different systems are, fundamentally, equally justified so long as they are a proper expression of the membership position that an object of nature possesses within the framework of the totality, for the dimension that was chosen as the basis for the particular system."
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> "The different systems . . . are not unrelated to one another. The relations between them . . . can themselves be made the subject of scientific systematic investigation. On the other hand, it is not basically a scientific task to combine several systems so created, because one and the same object cannot be presented and understood at the same time in its position as a member of different totalities."
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> W. Hennig (1966: 4)

Introduction

Darwin established the fact of evolution—the process of descent with modification—and its product, phylogeny. Although he predicted that taxonomies would become, "as far as they can be so made, genealogies" (Darwin, 1859: 486), the widespread acceptance of evolution did not lead to a major re-evaluation of the goals, principles and methods of taxonomy. Instead, existing taxonomies simply were reinterpreted in evolutionary terms. That is, the reality of previously recognized taxa was taken for granted and evolutionary concepts and mechanisms were formulated to account for their existence (Stevens, 1984; de Queiroz, 1988).

During the "modern synthesis" several authors, Mayr and Simpson in particular, explored the link between taxonomy and evolutionary theory. Their widely accepted conclusion was that species are fundamentally different from taxa at both higher and

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lower categorical levels. Species, unlike other taxa, are not only an outcome of evolution, they actually function in a direct way in the evolutionary process: as gene pools in the case of Mayr and as lineages extending through time in the case of Simpson. Species were seen to exist as wholes, that is, to be real things, whereas other taxa were viewed as subjective and arbitrary (Mayr, 1963: 600–601, 1969a: 91–92; Simpson, 1961: 188–191).

From the perspective of developing evolutionary systematics, perhaps the most significant aspect of the views of Mayr and Simpson was that existing species taxa were not taken as given. Although these concepts may have been formulated initially as theories to explain the existence of groups having common morphologies or ecologies, they quickly became prescriptions about how the species category should be defined, and as such they necessitated a re-evaluation of the status of existing taxa (Donoghue, 1985). Because the species category was defined in such a way that its members would be participants in the evolutionary process, the basal taxonomic unit became a fundamental evolutionary unit (e.g. Simpson, 1961; Hull, 1965, 1976; Mayr, 1969b, 1982).

This outlook contrasts sharply with an alternative view in which species concepts are treated as theories meant to explain the existence of already recognized taxa (e.g. Mishler and Donoghue, 1982: 494), a perspective that has hindered the development of systematics. By accepting the reality of previously recognized taxa, concepts associated with important biological processes are relegated to the role of after-the-fact explanations for the existence of these taxa, instead of functioning as central tenets from which real entities and the methods for their discovery are deduced (cf. de Queiroz, 1988).

Hennig (1966) did for the development of evolutionary systematics above the "species level" what Mayr and Simpson had done with regard to "species". That is, he changed the role of evolution as it relates to "higher" taxa, from an after-the-fact interpretation of the order already manifest in taxonomy to a central tenet from which he deduced what entities exist as its natural outcome (de Queiroz, 1985). According to Hennig, the products of evolution above the "species level" are groups composed of ancestral species and all of their descendants—complete systems of common ancestry—clades—monophyletic groups. Inasmuch as monophyletic groups are a natural outcome of the process of evolutionary descent, they are real and exist as wholes outside of the minds of taxonomists.

Hennig's concept of monophyly was seen by some later authors to have implications not only for taxa at "higher" categorical levels but also for those at the "species" level. In particular, Rosen (1978, 1979) and Bremer and Wanntorp (1979) argued that reproductive compatibility might be lost in a mosaic pattern among the populations descended from a common ancestor in such a way that the ability to interbreed, as a retained ancestral trait, would be uninformative about recency of common ancestry. Consequently, if organisms or populations were assigned to species taxa on the basis of this ability, then some species would be paraphyletic. This conclusion has led some authors to argue against species concepts based on interbreeding and to develop species concepts based on monophyly (Mishler and Donoghue, 1982; Cracraft, 1983, 1987; Ackery and Vane-Wright, 1984; Donoghue, 1985; Mishler and Brandon, 1987; McKitrick and Zink, 1988). They argue that there is not (or at least there should not be) a basic difference between species and other taxa; some monophyletic groups are simply more inclusive than others.

In short, a tension has developed around species concepts that involves ideas central to evolutionary biology in general and phylogenetic systematics in particular (cf. Løvtrup, 1987: 172–173). Here we explore some manifestations of this tension and their significance for phylogenetic systematics, especially as they bear on a choice among alternative species concepts. Nevertheless, we advocate neither a new species concept nor any existing one. Instead, we develop a way of *looking at* the species problem that builds upon the conceptualization of systematics expressed in the epigraph. Central to this view is a consideration of different kinds of entities that exist in nature and their relationships to one another.

Monophyly

Tension between the significance of interbreeding versus common descent is evident in discussions of the kinds of entities to which the concept of monophyly properly applies. Some arguments simply define the conflict out of existence. Platnick (1977), Willmann (1983) and Ax (1987), for example, considered it inappropriate to inquire whether species are monophyletic, paraphyletic or polyphyletic, claiming that these terms apply only to groups of species. This position unnecessarily restricts the concept of monophyly and overlooks the fact that species themselves are "groups" (groups of organisms). Regardless of precedents set by previous authors, there is no biological reason not to view monophyly, paraphyly and polyphyly as general concepts wherein the units of common ancestry are unspecified. Thus, these terms can be applied not only to groups of species but also to groups of any entities that reproduce and thus form ancestor–descendant lineages. Under this view it is legitimate to ask whether a particular organism is or is not a monophyletic group of cells, whether a particular population is a monophyletic group of organisms, or whether a particular species taxon is a monophyletic group of populations—as legitimate as it is to inquire whether a particular "higher" taxon is or is not a monophyletic group of species.

Wiley (1977, 1979) attempted to resolve the conflict between interbreeding and monophyly in another way. He claimed that species "are *a priori* monophyletic by their very nature" (Wiley, 1979: 214). In effect, his proposition is that because species have "a real existence in nature", therefore they are monophyletic. But this implies that there is only one kind of existence. If "species" and monophyletic groups exist in different ways, then "species" can exist without being monophyletic.

Other authors allow that it is legitimate to inquire whether species are monophyletic, but unlike Wiley they conclude that some species, namely ancestral ones, are paraphyletic. Brothers (1985) coupled this idea with the notion that asexual organisms form evolutionary species (*sensu* Simpson, 1961; Wiley, 1978) and concluded that paraphyletic higher taxa are meaningful evolutionary groups. This follows from his assertion that the relationship between asexual species and their component organisms is analogous to that between higher taxa (including paraphyletic ones) and their component species.

Brothers's argument hinges on the false premise that paraphyletic sexual and asexual "species" exist in the same way. Paraphyletic asexual "species", however, are not unified by interbreeding as are sexual "species"; instead they are defined solely by phenetic similarities and gaps (Brothers, 1985: 36). In fact, the only connection between sexual and asexual "species" in Brothers's argument is that both are supposedly accommodated under the evolutionary species concept. The evolutionary species concept (Simpson, 1961), however, refers to "a single lineage of ancestral descendant populations" (Wiley, 1978: 18), and to equate the kinds of lineages formed by sexual and asexual organisms under the term "evolutionary species" is to confuse two different uses of "population". Only the unjustified acceptance of phenetically delimited, paraphyletic collections of asexual organisms as "real evolutionary species" supports Brothers's contention that paraphyletic higher taxa are acceptable evolutionary groups (see Donoghue, 1987, for additional discussion).

The arguments of Wiley and of Brothers are similar in one important respect—both tacitly assume that different kinds of entities exist in the same way: monophyletic groups and "species" in the case of Wiley; sexual and asexual "species" in the case of Brothers. Others, for example Eldredge and Cracraft (1980), have argued that there is a fundamental difference between sexual species and monophyletic higher taxa. They allow that some species, namely ancestors, are not monophyletic, but they consider this to be acceptable because species exist in a different way, namely as individuals. For Eldredge and Cracraft (1980: 90), monophyletic groups exist but are not necessarily individuals, whereas species exist *because* they are individuals.

Individuality

The concept of individuality has figured prominently in many recent discussions of species concepts, including several of those discussed above. That organisms are not the only kind of biological "individuals" follows from accepting that living matter is organized into wholes that are themselves parts of more inclusive wholes. Although Ghiselin (1966, 1974, 1981, 1985) and Hull (1976, 1977, 1978) deserve credit for popularizing and developing the idea that species are appropriately viewed as individuals in the philosophical sense, very similar ideas were set forth independently by Hennig (1966) and Griffiths (1974), whose discussions of the individuality of biological taxa stem from the writings of even earlier authors (i.e. Woodger, 1952; Gregg, 1954).

The concept of individuality is commonly illustrated by contrasting individuals with classes and describing characteristics of each (Ghiselin, 1974; Hull, 1976, 1977, 1980, 1981). Classes have members; individuals have parts. Classes are spatiotemporally unrestricted; individuals are localized in space and time. The names of classes are usually defined "intensionally" (i.e. by listing the attributes that are necessary and sufficient for membership); the names of individuals are proper names and can only be defined "ostensively" (i.e. by showing the object to which the name is given). The members of a class are similar in that they share at least the attributes that define the class name; the parts of an individual need not be, and frequently are not, similar. Beyond this general characterization, however, there are more and less restricted concepts of individuality. Thus, according to Hull (1978) and Wiley (1981) individuals must not only be spatiotemporally localized but also must be continuous and cohesive. These last two terms require special attention as they bear directly on the existence of different kinds of entities that have organisms as parts.

CONTINUITY

There are at least two different forms of continuity: current and historical. Wiley (1981) made current continuity an explicit component of his concept of individuality. He did not, however, distinguish between current continuity and cohesion, for he considered both to result from the same process (at least in sexual species), namely reproductive ties among organisms. In contrast, Ghiselin (1974) explicitly rejected current continuity as a necessary component of individuality, arguing that the United States of America is an individual nation despite the physical discontinuity between Alaska and the remainder of the continental United States. The truth of this example notwithstanding, at least some kinds of individuals (e.g. multicellular organisms) result from direct physical connections among their parts, and in these cases continuity is inescapable. It appears, then, that whether current continuity is a necessary component of individuality depends upon the nature of the phenomenon conferring individuality.

Historical continuity has been identified as the unbroken chain of descent from a common ancestor (e.g. Ghiselin, 1980; Wiley, 1981). While this applies to some kinds of individuals (e.g. monophyletic groups) it does not seem to be a necessary component of individuality. An organism, for example, does not cease to be an individual when it receives an organ transplant, nor does a population of interbreeding organisms cease to be an individual when it receives immigrants. As in the case of current continuity, it seems that whether historical continuity is necessary for individuality depends on the nature of the phenomenon conferring individuality.

Cohesion

The presence or absence of cohesion has been considered an important difference between "species" and monophyletic higher taxa (e.g. Hennig, 1966; Wiley, 1981; Ghiselin, 1985). Unfortunately, ambiguities still plague this critical issue, some of which are clarified by considering the meaning of "cohesion" and the biological phenomena that might confer it.

"Cohesion" is commonly used to mean "sticking together" (e.g. *Webster's New International Dictionary*, 2nd edn); thus, cohesion is a property that might confer individuality by uniting parts to form a whole. The cells that make up a multicellular organism are physically stuck together, but at the "species level" cohesion is less obvious. According to Wiley (1981), cohesion among the parts of a species composed of sexually reproducing organisms is maintained by reproductive ties (see also Brooks and Wiley, 1986: 48–49). In contrast with the biological species concept (e.g. Mayr, 1942), however, only actual interbreeding matters in this context (cf. Hull, 1965). If cohesion is conferred by interbreeding, then the potential to interbreed allows only the potential to cohere. That interbreeding is widely considered to be the process conferring "species level" cohesion is evident from the commonly stated view that asexual organisms do not form "species" (e.g. Bernstein et al., 1985). As Hull (1980) put it, "strictly asexual organisms form no higher-level entities; organism lineages are the highest level lineages produced."

Other than sexual reproduction, no biological process has been identified that might confer cohesion at the "species level". Although interactions other than interbreeding seem to confer cohesion on groups of organisms that make up colonies or symbiotic partnerships, these entities are never called "species". Several other phenomena have been suggested as "species level" agents of cohesion, but such proposals confuse cohesion with constraint or inertia. Wiley (1981), for example, considered that stasis maintains cohesion among the parts of "species" composed of either sexual or asexual organisms (see also Mishler, 1985; Mishler and Brandon, 1987). Stasis may result from either extrinsic or intrinsic *constraints*, such as stabilizing selection or the resilience of developmental systems. Although such phenomena may cause organisms to remain similar, this is not the same as "sticking together". When discussing biological individuals having organisms as their parts, cohesion must refer to interactions among those organisms. Shared genetic or developmental programs, or common mate recognition systems (Paterson, 1978, 1985), or any other properties that organisms might have in common, no matter how biologically significant, are not interactions among those organisms.[1] Although some of these properties may allow cohesive interactions to occur among organisms, they do not, by themselves, constitute cohesion.

Although cohesion has often been associated with individuality, it is not required by every version of the concept. Thus, according to Ghiselin (1974) an individual is simply "a particular thing". This is compatible with the view taken by Hennig (1966), Patterson (1978), Ghiselin (1969, 1980, 1985), Griffiths (1974) and Hull (1976) that monophyletic higher taxa are individuals, despite the fact that they do not exhibit cohesion among their parts, each being made up of independently evolving lineages (Wiley, 1980, 1981). Wiley (1980, 1981) stressed this basic distinction by coining the term "historical group" for monophyletic higher taxa (which are historically continuous), and restricting "individual" to cohesive entities such as "species". Ghiselin (1985) accepted this distinction, but preferred a classification in which "individual" includes both non-cohesive historical groups and cohesive units (which he called "integrated wholes").

We conclude that several different kinds of entities have been called individuals. Consequently, the individuality "revolution" (Ghiselin, 1987) may be partially responsible for obscuring significant distinctions between them. The view has developed that individuals are things with a real existence in nature; for this reason, if something is said to be an individual it seems to gain significance. Simply asserting that something is an individual, however, does little to clarify the nature of its existence. Inasmuch as one kind of individual may be significant for one theory but not for another, it is necessary to go beyond individuality and answer the question "individual what?". In the next section our aim is to focus attention away from individuality *per se* and instead to explore those phenomena that confer existence on certain entities that have been identified as individuals.

Systems

The nature of existence of wholes is clarified by adopting the perspective of systematics formulated by Griffiths (1974) and has been discussed recently by de Queiroz (1988). These authors distinguished between classification, the ordering of entities into classes, and systematization, the ordering of entities into systems. Classification and systematization differ fundamentally in that classes are groups whose members belong to those groups because they share some attribute(s), whereas systems are wholes that derive their existence from some natural process through which their parts are related (de Queiroz, 1988). Ghiselin (1974) pointed out that the term "individual" can designate systems at various levels of integration, which suggests that the different kinds of entities previously identified as individuals might be viewed as kinds of wholes

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[1] Vrba (1985) suggested a "fundamental compatibility between the 'individual' and 'recognition concepts' of species", at least in part because both "draw on the reproductive activities among organisms". Nevertheless, under Paterson's recognition concept, species are classes defined by similarities and differences in characters that make fertilization *possible*; actual reproduction, or even actual mating, are not required (see Donoghue, 1987).

deriving their existence from different underlying natural processes. This perspective facilitates discrimination among different kinds of individuals by focusing directly upon the natural processes responsible for their existence.

We have identified two processes through which organisms are related: interbreeding and common descent. Exploration of the systems resulting from these different processes and the relations between them is facilitated by constructing a table with interbreeding (resulting in one kind of cohesive whole) along one axis and common descent (resulting in monophyletic groups) along the other (Fig. 1). Entities in the upper left-hand box of this table (labeled I) are both cohesive and monophyletic, entities in the lower left-hand box (II) are cohesive but not monophyletic, and so forth. The word "individual" has been applied by one author or another to entities in each of the first three boxes. Any entities in box IV are either systems deriving their existence from some natural process other than interbreeding or common descent, or they are recognized simply because their members share certain traits and therefore are classes. In the latter case, regardless of the importance of the traits upon which such groups are based, they do not qualify as systems. Unless their parts are related through some natural process, such classes do not exist as wholes. Included here are paraphyletic and polyphyletic higher taxa, which must be viewed either as aggregations or collections of less inclusive wholes, or as parts (incomplete systems) of more inclusive wholes.

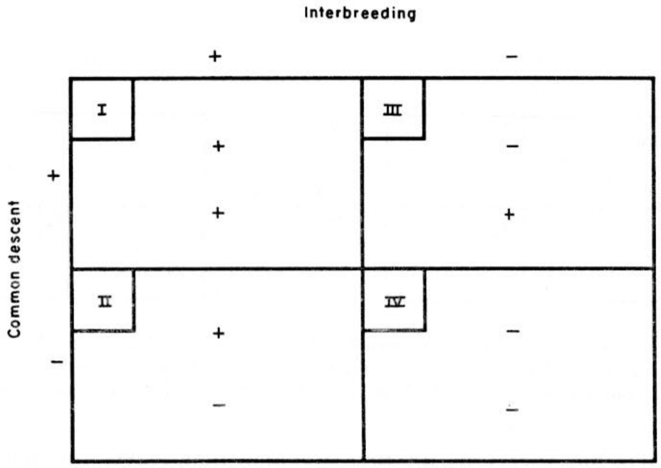

Fig. 1. Possible relations between cohesive wholes resulting from the process of interbreeding and monophyletic groups resulting from the process of common descent. Presence of each process is symbolized by + and absence by −.

Because two different processes are being considered, a group of entities that forms a system resulting from one of the processes may or may not also form a system resulting from the other (cf. Holsinger, 1984). This point is easily visualized by using the table in Fig. 1 to follow groups of entities through time (Fig. 2). Suppose, for example, that we begin with a gravid female of some kind of sexually reproducing organism. She and her offspring establish a population within which there is steady interbreeding between component organisms. For the sake of simplicity, let us further suppose that no deaths occur. For a time this population resides in box I—it is both a monophyletic group of organisms and a group that is cohesive as a result of interbreeding (Fig. 2a). Now

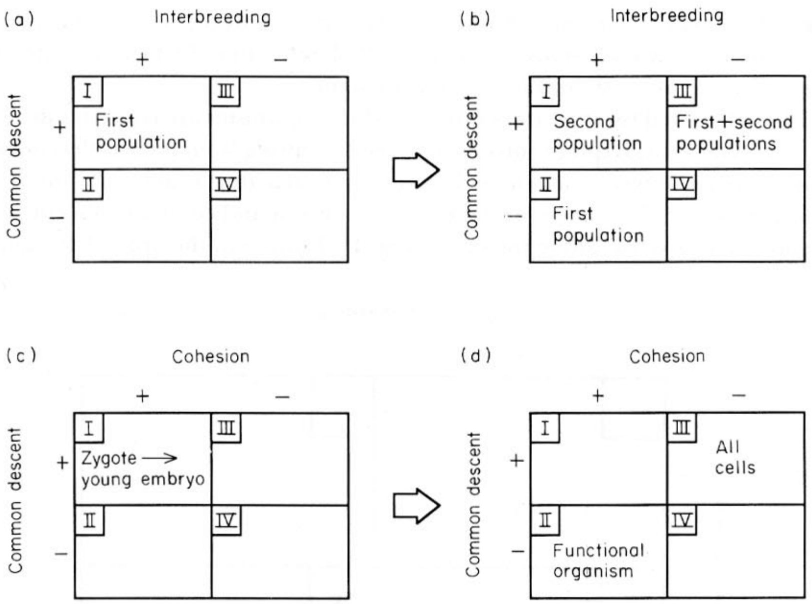

Fig. 2. Entities followed through time as categorized in the table in Fig. 1. (a) A young population descended from a single gravid female. (b) System (a) after the establishment of a new population. (c) A young embryo descended from a single zygote. (d) System (c) after some cells have died and been sloughed off.

imagine that at some later time another gravid female leaves this population and successfully establishes a new population that is geographically separated from the first, so that the two populations are reproductively isolated by distance. At this point (Fig. 2b) the first population shifts into box II—it is no longer a monophyletic group of organisms; however, it remains a cohesive entity. The first and second populations, taken as a unit, now occupy box III, because together they constitute a monophyletic but non-cohesive group. Finally, the newly established population begins its existence in box I.

The point of this exercise is that there may be switches between boxes or states of existence, and one is free to focus attention on entities belonging to any of the classes in the table of possibilities. Thus, we might choose to focus on interbreeding systems, on those resulting from common descent, or on both. There is no right or wrong in this; one is not better than another, or generally more significant. The entities in the upper row of boxes and those in the left-hand column all exist, but they exist in different ways, that is, they exist as the outcome of different processes. Furthermore, in box I, wholes deriving their existence from one of the processes correspond precisely with (have the same parts as) wholes deriving their existence from the other process.

It is worth noting that the framework developed above is a general one, which is to say that other forms of cohesion and common descent may occur at different levels of organization. For example, instead of following groups of organisms one might focus on groups of cells (Fig. 2c,d). Following the first few mitotic divisions, the group of cells making up an embryo is integrated into a cohesive whole by physical and chemical interactions; these also form a monophyletic group of cells descended from the zygote. This group of cells therefore exists in box I (Fig. 2c). At a later time during development (Fig. 2d) some cells die and are sloughed off the embryo (or perhaps the embryo is split into two cohesive wholes as in the case of identical twins). After this point we might choose to follow the fate of the functioning organism, which remains a cohesive whole but is no longer a monophyletic group of cells. Alternatively, we might focus on the set of *all* cells descended from the zygote, even though these are no longer all integrated in one functioning body.[2] Traditionally, attention has been focused on the cohesive organism, but there may be some purposes for which it is necessary to keep track of the monophyletic group of cells; for example, in studying the frequency of somatic mutations.

The foregoing analysis emphasizes that the tension surrounding species concepts results from there being different kinds of real biological entities. Some of these entities exist as an outcome of a process conferring cohesion, while others exist as an outcome of descent from a common ancestor. And sometimes an entity that exists as the consequence of one of these processes happens to correspond exactly with one that exists as a consequence of the other. Before we can explore how these conclusions bear on the species problem, it is first necessary to examine some assumptions and limits of phylogenetic systematics.

Phylogenetic Systematics

Adopting the view that systematics is the discovery of entities that derive their existence from some underlying natural process implies that phylogenetic systematics is that kind of systematics in which the process of interest is evolutionary descent (de Queiroz, 1988). The methods of phylogenetic systematics are based on the premise that there exists an evolutionary tree and, therefore, a nested hierarchical pattern of relationships. This implies that it is inappropriate to apply cladistic methods to entities that are expected *not* to be related in a nested hierarchical pattern, that is, entities related in some other pattern, such as a reticulum of intersecting sets. In other words, there are identifiable limits to the sensible application of phylogenetic methods, boundaries beyond which it is fruitless to proceed.

The exact nature of these limits depends on the properties of the entities under investigation. In the case of sexually reproducing organisms a limit is set by the level at which continually branching (diverging) relations give way to predominantly reticulate relations resulting from interbreeding. It is inappropriate to inquire about phylogenetic relationships among actually interbreeding organisms, because here the pattern of relationships is not a nested hierarchy (cf. Hennig, 1966: 18–19). Phylogenetic methods break down in this case because an assumption underlying the principle that shared derived characters provide evidence of phylogenetic relationship (i.e. of monophyly) is violated. Thus, in the case of sexual dimorphism, grouping by shared derived characters may lead to the false conclusion that the males (for example) within a population of interbreeding organisms form a monophyletic group. The problem in this case is that sex-linked traits of the males are being interpreted as synapomorphies at the wrong level, a fact that would become evident upon examining the distribution of these traits among parents and their offspring.

Populations themselves, in contrast with their component organisms, may show a

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[2] A monophyletic group consists of an ancestor and all of its descendants. Thus, the dead and sloughed cells are part of the monophyletic group of cells descended from the zygote, although they are no longer part of the functioning organism. Similarly, monophyletic groups of organisms include dead organisms, even though these are no longer parts of interbreeding populations, and monophyletic "higher taxa" include extinct and unknown subgroups.

branching pattern of relationship to one another. Indeed, using populations as terminal taxa will potentially yield the finest possible resolution of phylogenetic relationships among sexually reproducing organisms. Populations, therefore, have a special role as "basal units" in the phylogenetic systematics of organisms.[3] This role is entirely independent of whether these units are monophyletic, but instead is an outcome of the process of interbreeding.

In the case of organisms that reproduce only asexually the limits of phylogenetic analysis are different. Here, in contrast with the reticulate relationships that result from sexual reproduction, the pattern of common ancestry among asexual organisms forms a nested hierarchy. Whether asexual organisms are monophyletic or paraphyletic groups of cells, relationships among them are amenable to phylogenetic analysis because these organisms are cohesive wholes that form diverging lineages.[4]

Hennig (1966: 29–32) delimited the scope of phylogenetic systematics in distinguishing parts of "the total structure of hologenetic relationships". His figure 6 (our Fig. 3) shows semaphoronts linked into semaphoront groups (individual organisms) through ontogenetic relationships, and organisms linked through "tokogenetic relationships" into species. Phylogenetic relationships were limited by Hennig to those above the level of interbreeding groups—to relationships among "species". Most of Hennig's discussion assumed a sexual mode of reproduction. Regarding cases of asexual reproduction he noted that the differences between ontogenetic, tokogenetic and phylogenetic relationships are blurred. Nevertheless, he concluded that even in asexual groups "it is possible to delimit in the fabric of hologenetic relationships an area that lies between the more or less unequivocally phylogenetic relationships on the one hand and the ontogenetic relationships on the other", and that "this area naturally corresponds to the species category of organisms with bisexual reproduction" (Hennig, 1966: 44).

Hennig's discussion of hologenetic relationships in sexual organisms is insightful, as is his recognition that the difference between reproduction and development is not always entirely clear in the case of asexual organisms (cf. Janzen, 1977, and the "genet"/"ramet" terminology of botanists, e.g. Harper, 1977). Nevertheless, we disagree with his views on the status of asexual "species" and the limits of their phylogenetic relationships. In asexual organisms tokogenetic relationships have a fundamentally different structure than they do in sexual forms, each organism being the direct descendant of one rather

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[3] Throughout this paper we mean by "population" units within which interbreeding between organisms of different subunits is sufficient such that the relationships among these subunits are reticulate, while relationships among the units themselves are predominantly diverging. Consequently, the units that qualify as populations depend upon the time scale under consideration. Over short time periods, there may be a diverging pattern of relationships among demes, and this is potentially recoverable through cladistic analysis. This pattern of relationships, however, may be obliterated over longer periods of time if there is sufficient gene flow among demes so that they function together as a single population.

[4] The cohesion responsible for the existence of individual organisms, whether sexual or asexual, does not involve reticulate patterns of descent among their component parts. Therefore, phylogenetic analysis can be extended down to the level of cells, or even to parts of cells (e.g. organelles, chromosomes, "genes"). This is done, for example, in analysing the propagation of somatic mutations within and between the meristems of plants (Whitham and Slobodchikoff, 1981; Klekowski et al., 1986; see Buss, 1983, 1987, for examples in animals). However, parts that reproduce can begin diverging prior to the divergence of more inclusive wholes. This occurrence, in conjunction with differential sorting of variant parts within higher level lineages, can result in non-correspondence between phylogenetic relationships among entities at different levels (Kawata, 1987). For example, mitochondria, which form lineages perpetuated through maternal germ cells, can exhibit different patterns of phylogenetic relationships from the populations of organisms in which they reside (Neigel and Avise, 1986).

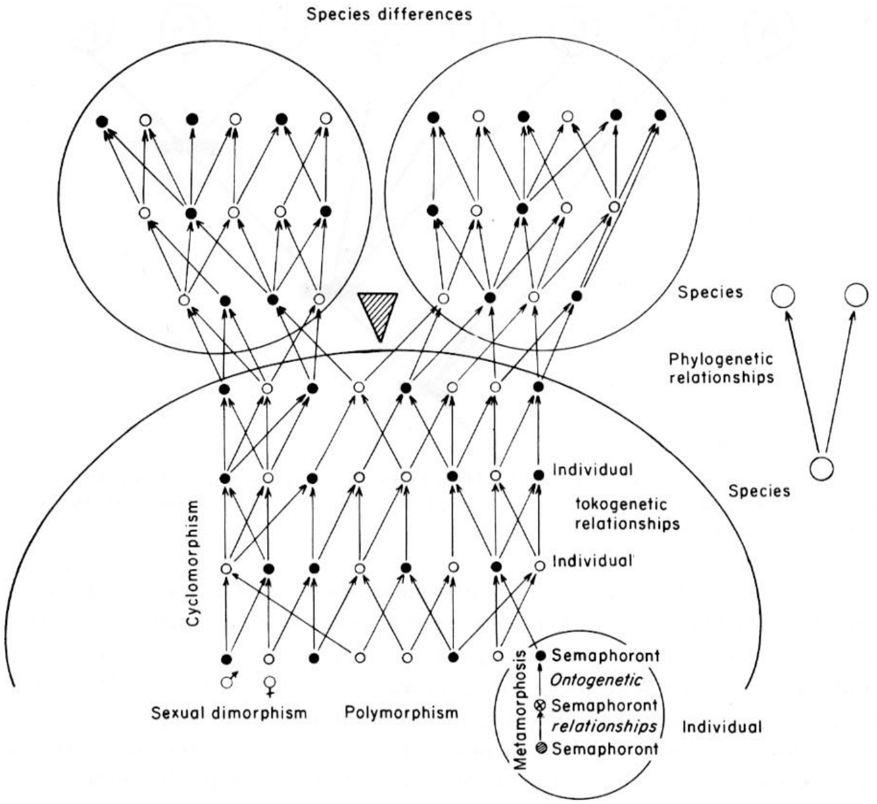

Fig. 3. Figure 6 after Hennig (1966: 31): "The total structure of hologenetic relationships and the differences in form associated with its individual parts" (reprinted with the permission of University of Illinois Press).

than two parents. In such cases there are no systems deriving their existence from interbreeding as there are in sexually reproducing organisms. Consequently, in obligately asexual groups phylogenetic relationships correspond precisely with tokogenetic relationships, both being relationships among individual organisms (i.e. life cycles *sensu* Bonner, 1974).

Species

If we endeavor to practise systematics in the sense of Griffiths, then species names (or the names of any systematic taxa) should refer to the individual members of one of the classes of entities that exist as the outcome of some natural process. But this still leaves open different possibilities, because distinct classes of entities relevant to phylogenetic systematics derive their existence from both interbreeding and common descent.

We will illustrate these possibilities with a hypothetical situation. Suppose that we have identified all of the separate populations within a particular monophyletic group and that the phylogenetic relationships among these populations have been assessed using cladistic methods (Fig. 4). In actuality, the relationships might be more completely resolved than those shown in Fig. 4, but for the sake of the following discussion we will assume that the organisms in some of the populations are not differentiated from one another and therefore some relationships cannot be resolved.

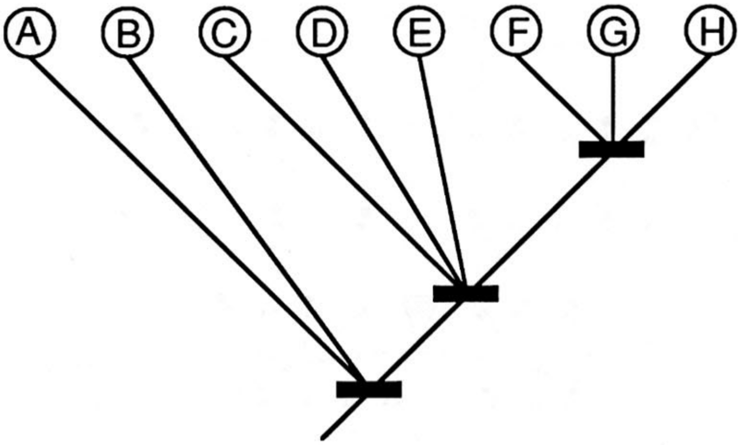

Fig. 4. A cladogram of eight populations (A–H); interbreeding occurs within each population, but among populations it does not. Although certain monophyletic groups of populations exist, the populations themselves are not necessarily monophyletic.

Indeed, we expect that cladograms of populations will often be less than fully resolved (Arnold, 1981; Donoghue, 1985; also see discussion below of direct ancestry under "Species Concepts Based on Monophyly"). This case provides a framework for considering several possibilities for the application of the term "species". We will use it to illustrate the consequences of adopting each of several alternative species concepts. It is not our intent, however, to advocate one of these concepts over the others. Instead, we accept the validity of each one and explore its implications for phylogenetic systematics and taxonomic conventions.

Species Concepts Based on Interbreeding

One possibility, which might be considered even without any knowledge of cladistic relationships, would be to apply species names to each of the eight separate populations (A–H, Fig. 4). This alternative focuses on the systems that exist as a result of interbreeding at the present time, without considering what might happen to them in the future or their phylogenetic relationships to one another. In effect, this is a narrow version of the biological species concept.

Equating species with actually interbreeding groups of organisms would be useful to many biologists, since these entities are presumed to play a special role in the evolutionary process (e.g. Futuyma, 1986). Furthermore, the entities recognized as species under this concept are significant from the perspective of phylogenetic systematics since, as we argued above, populations are the least inclusive units appropriate for use as terminal taxa when analysing phylogenetic relationships among sexually reproducing organisms.

In view of the fact that populations are not always monophyletic, this concept might appear to entail a double standard concerning the criterion of monophyly. This is not the case. In keeping with the tradition in which species are seen as fundamentally different from other taxa, the names of species simply would designate an entirely different kind of entity than the names of other taxa in the phylogenetic system (de Queiroz, 1988). The "higher" taxa, as systems of common ancestry, would be members of the category "monophyletic group", but members of the species category, as interbreeding systems, might not be monophyletic. In short, there would be two different classes of systems formally recognized as taxa. That groups of actually interbreeding organisms are not always monophyletic is not, by itself, a reason to avoid designating such groups as species; evolutionary descent is not the only process through which organisms are related, nor is monophyly the only form of existence.

Perhaps the main difficulties with this species concept are practical ones. It is often very difficult to determine the limits of actual interbreeding, especially since the degree of gene flow varies in space and time and there need be no correspondence between interbreeding and morphological or ecological divergence (Mishler and Donoghue, 1982; Donoghue, 1985). Beyond this methodological problem, adoption of this concept would probably lead to conflicts with traditional species taxa. If species names were applied to all separate populations, there would be many more species than are currently recognized. Furthermore, organisms that reproduce exclusively by asexual means could not be considered to be parts of species.

There is a well known alternative to applying species names to actually interbreeding groups of organisms, namely to have species names represent potentially interbreeding groups of organisms—the broad (and standard) version of the biological species concept. This alternative is conceptually related to the first, and because there is presumably a continuum of reproductive interactions—from frequent to rare to none at all—these two concepts grade into one another.

In order to explore this alternative, suppose that in addition to the information represented in Fig. 4 we also know the potential of organisms in each of the eight populations to interbreed with one another and produce fertile offspring. In particular, suppose that members of populations A through E can successfully interbreed (even though they are not actually interbreeding), and that members of populations F through H also can interbreed among themselves, but that interbreeding is not possible between organisms from the two different groups of populations (Fig. 5). If the species category is defined on the basis of the potential to interbreed, then species names would be given to these two groups of populations (A–E and F–H).

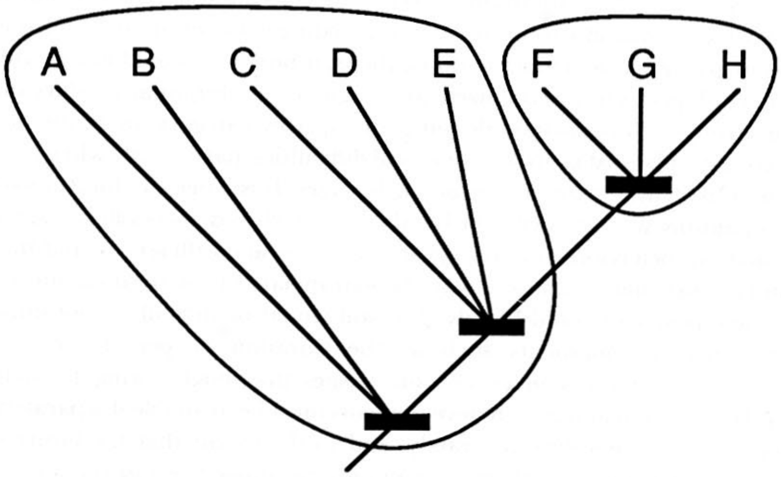

Fig. 5. A cladogram of separate populations (as in Fig. 4) showing potentially interbreeding groups. Organisms within the enclosed groups of populations (A–E and F–H) can potentially interbreed; interbreeding is not possible between organisms from the different groups.

Delimiting species on the basis of the potential to interbreed is appealing in that it attempts to capture the idea that species exist through evolutionary time rather than being manifestations of current gene flow. Moreover, loss of the potential to interbreed guarantees that the entities are functioning as separate evolutionary units. In these respects, the potentially interbreeding species concept is similar to the evolutionary species concepts of Simpson (1961) and Wiley (1978), which emphasize the existence of species through time by viewing them in terms of their fates as lineages. One might argue, for example, that populations among which there is potential but currently no actual interbreeding might come back in contact in the near future, at which time there would be sufficient gene flow that the populations would fuse and any differentiation between them would disappear. In other words, given enough time, these populations would be in contact often enough that they would function together as a single unit in evolution.

Despite this appeal, defining the species category in terms of potential interbreeding also has theoretical drawbacks. Units recognized strictly on this basis need not be, and perhaps often will not be, cohesive in the short run or even in the long run. Species based on potential interbreeding may be simply collections or classes, the members of which are functioning and will always function as separate units in the evolutionary process. Consequently, the processes responsible for "speciation" (i.e. irreversible reproductive closure) under this concept are not necessarily the same as those responsible for the origin of separate evolutionary units. Furthermore, as noted earlier, potentially interbreeding groups defined solely by the retained ability to interbreed might be paraphyletic, in other words, they might not be systems of common ancestry any more than interbreeding systems. Such demonstrably paraphyletic groups (e.g. populations A–E in Fig. 5) obscure information on common ancestry, which in turn hinders the study of historical biogeography and character evolution. It is not clear how the recognition of such units, which are neither cohesive nor monophyletic, and which are delimited on the basis of what might or might not occur in the future, can be used in testing theories about evolutionary processes (W. Maddison in Vlijm, 1986).

Potential interbreeding as a criterion for circumscribing species has practical advantages over the first alternative, because it avoids the technically difficult task of assessing which organisms are actually interbreeding with one another. Furthermore, in contrast to giving species names to populations, it probably would not greatly increase the number of species now recognized, and might even substantially reduce the number in some groups. Nevertheless, defining the species category in terms of potential interbreeding is plagued by its own practical difficulties, particularly when it is viewed as an attempt to identify separately evolving lineages. It is, after all, difficult to determine which organisms will and will not be able to interbreed successfully on the basis of morphological, behavioral, or ecological similarities and differences, and the results of laboratory experiments cannot always be extrapolated to natural circumstances. But even if these problems could be solved, it still would be difficult, if not impossible, to predict future developments such as the duration of persistence of potential interbreeding or changes in geographic ranges that might bring populations into contact. Information about such developments must be available if separately evolving lineages are to be identified accurately, and to the extent that the future cannot be predicted, lineage concepts of species can only be applied retrospectively.[5]

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[5] Throughout this paper, "lineage" refers to a single ancestor–descendant sequence and is not to be equated with "monophyletic group". Monophyletic groups are often composed of multiple lineages (de Queiroz, 1988).

Species Concepts Based on Monophyly

A second set of possibilities focus on evolutionary descent. Here species taxa are some subset of those groups thought to be monophyletic, whether or not they are cohesive. Thus, species would be systems of the same sort as "higher" taxa in the phylogenetic system, and the species category would designate one rank in a hierarchy, all the ranks of which would be applied to monophyletic taxa. The process of delimiting such species might proceed as before, with the identification of appropriate basal units (populations in the case of sexually reproducing organisms) and the assessment of phylogenetic relationships among them (Fig. 4). Under the requirement that all taxa, including species, be monophyletic groups, the groups labeled I, II and III in Fig. 6 would qualify.

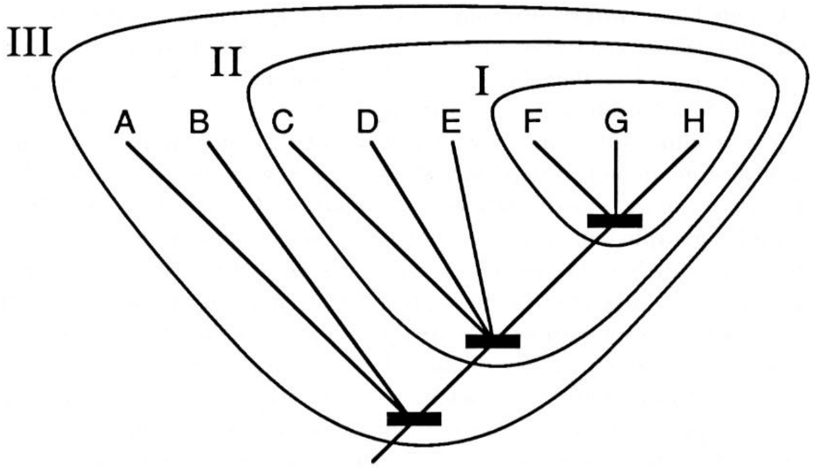

Fig. 6. A cladogram of separate populations (as in Fig. 4) showing three monophyletic groups of populations (I–III).

But which one(s) of these monophyletic groups ought to be assigned to the species category?

One possibility is to recognize as species all and only the smallest (least inclusive) monophyletic groups—either individual populations or groups of populations. In our example, the clade labeled I would therefore be recognized as a species, but clades II and III could not be species for at least two reasons. First, they are not the smallest monophyletic groups, and second, recognizing one or both of them (as well as clade I) as species would result in species nested within one another, which would take away the meaning of categorical ranks altogether. Thus, if clade I is a species, then clades II and III must be "higher" taxa, in which case the lowest ranking monophyletic taxon to which any of the populations A through E could be assigned would be a "higher" taxon. In short, it will be possible to assign all organisms/interbreeding populations to one or more monophyletic taxa, but it will not be possible to assign all such entities to monophyletic taxa of species rank.

This conclusion is not simply a function or having chosen at the outset to recognize only the smallest monophyletic groups as species; the same result obtains even when more inclusive monophyletic groups are recognized as species. For example, we might choose to recognize clade II as a species, but then it would not be possible to assign populations A and B to a monophyletic taxon of the species category. Neither does the problem result from incomplete information about phylogeny, for some population(s) may be ancestral to others, and hence paraphyletic. Although identification of ancestral populations is generally a difficult task, such populations presumably exist. Even if their status as direct ancestors cannot be demonstrated, they are likely to appear in cladograms as parts of unresolved polytomies or as single branches without diagnostic apomorphies.

Although not assigning all organisms or populations to taxa of species rank violates a longstanding convention, this alone is insufficient grounds for rejecting a definition of the species category based on monophyly. If the goal of systematics is to depict relationships accurately, then any traditions that interfere with this goal should be abandoned.

There is, however, a way of emphasizing monophyly in the definition of the species category while also providing for the assignment of the vast majority of organisms to species taxa. This is achieved by introducing a convention that allows the recognition as species of single basal entities, or groups of basal entities, whose monophyletic status is uncertain (Donoghue, 1985). For example, the relationships of populations C, D and E in Fig. 4 are unclear. Together they may form a monophyletic group or this group may be a paraphyletic assemblage—characters support neither hypothesis (Fig. 7). Following Donoghue (1985) and Gauthier et al. (1988), potential paraphyly should be distinguished from demonstrated paraphyly in which there is evidence that some populations are more closely related to populations placed in another taxon. Demonstrably paraphyletic groups would not be recognized as taxa under this convention. Nevertheless, the following kinds of groups might be recognized temporarily on the grounds that they may be monophyletic: (1) populations lacking autapomorphies, or (2) groups of populations that are not differentiated from one another and that lack the diagnostic apomorphies of any clade(s) nested within the least inclusive monophyletic group to which they belong (e.g. the group of populations [C, D, E] in Fig. 6). If this proposal were adopted it might be desirable to give such groups of uncertain status a special designation (Donoghue, 1985, proposed "metaspecies" and suggested that their names be marked with an asterisk). These measures are intended to ensure that such taxa would be treated cautiously until their relationships are better understood. The "metaspecies" convention allows an unambiguous reflection of phylogenetic relationships, insofar as these are known, while also allowing unresolved groups of organisms to be assigned to taxa of species rank.

Nevertheless, if the criterion of monophyly is to be applied consistently to basal entities as well as to groups of such entities, then it still would not be possible to recognize as species (or monophyletic taxa of any rank) populations that are known to be ancestral to others (perhaps through direct observation of an immigrant establishing a new population). Such populations are paraphyletic (although not necessarily as evidenced by characters) and therefore would not be covered by the metaspecies convention because they contradict the fundamental idea of a species concept based on monophyly. As pointed out by Hennig (1966: 71), an ancestral species, before it gives rise to any descendants, is equivalent (as a monophyletic group) to the group composed of itself and all the species descended from it considered at a later time. Thus, the ancestral population of a monophyletic group recognized as a genus is part of that genus but not of any less inclusive monophyletic taxon. Nevertheless, given the difficulty of identifying ancestors (Wiley, 1981), leaving these unassigned to taxa of species rank is unlikely to cause great practical problems.

The case in which "species" refers to the least inclusive monophyletic groups has several other practical difficulties. One problem is that it is not an easy task to construct cladograms using populations (or organisms) as terminal units (cf. Arnold, 1981), and

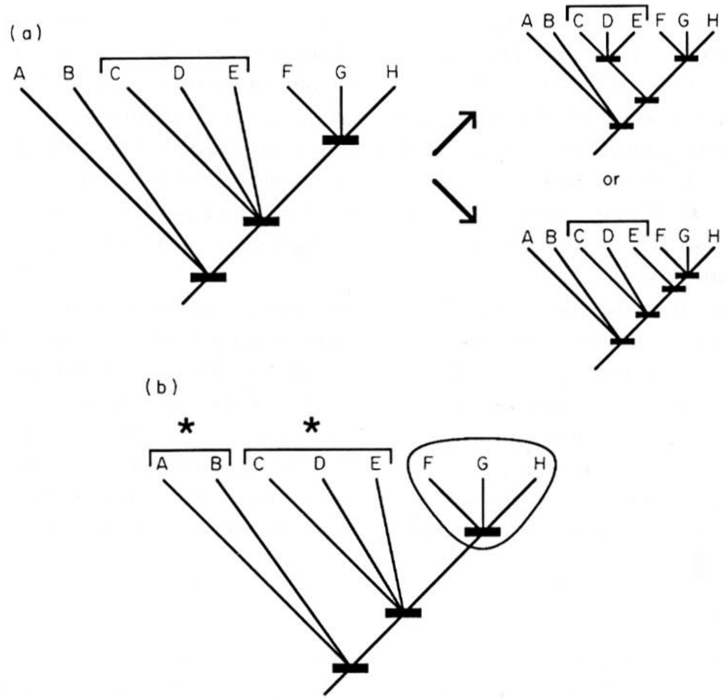

Fig. 7. Cladograms of populations (as in Fig. 4). (a) Possible resolutions of the unresolved group of populations C–E. In the upper resolution, C–E is found to be monophyletic; in the lower resolution, C–E is found to be "positively" paraphyletic. (b) Application of the "metaspecies" convention, where asterisks symbolize metaspecies A–B and C–E; populations F–H form a "positively" monophyletic species.

this degree of resolution is far from being achieved in most groups. Another problem is that there would probably be more species recognized if this approach were adopted than we are presently accustomed to; for example, many groups that are presently accorded subspecific ranks would qualify as species (Cracraft, 1983). In asexual organisms the situation would be even more extreme.

A more general objection to defining the species category as one level in the hierarchy of monophyletic groups arises from considering the usefulness of categorical ranks. Linnaean taxonomy requires two distinct activities: grouping, the discovery/identification of groups, and ranking, the assignment of a Linnaean categorical rank to each one of these groups (Donoghue, 1985).[6] In systematics (*sensu* Griffiths), the activity of grouping corresponds with systematization itself, but the significance of ranking is less clear. Although monophyletic taxa exhibit a nested, hierarchical pattern of relationships, which is exactly the same kind of pattern used in Linnaean taxonomies, categorical ranks add no information about monophyly that is not already contained in a cladogram or an indented taxonomy (Eldredge and Cracraft, 1980; Gauthier et al., 1988).

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[6] The term "grouping" is unfortunate in that it seemingly implies that the "groups" are formed by some human activity, rather than existing independently and being discovered by humans. Furthermore, the term "group" itself, as in "monophyletic group" and "historical group", is unfortunate in that it seems to imply that such entities are collections rather than more inclusive wholes. At best, such usage reflects viewing the whole not from its own level but from the level of the less inclusive entities (parts) of which it is composed.

There is also the problem that the very existence of categorical ranks encourages spurious comparisons between entities assigned the same rank but that are not otherwise comparable (Gauthier et al., 1988). One possible solution to this problem is to have ranks reflect the absolute ages of groups (Hennig, 1966), but this proposition has not been accepted by most systematists. Another possibility suggested by Hennig (1969) and Griffiths (1974, 1976), among others, is that the categorical ranks of Linnaean taxonomy be abandoned. If ranking serves no purpose other than perpetuating tradition, the difficulties associated with it provide a compelling reason for considering the possibility of abandoning ranks.

It is ironic that the possibility of eliminating ranks, which arose from considering "species", like other taxa, to be monophyletic groups, reopens the alternative of a species concept based on interbreeding. If "species" simply denotes one hierarchical rank within the category "monophyletic group", and if ranks are unnecessary, then why should some monophyletic groups be called "species". In other words, while the abandonment of categorial ranks in no way hinders the representation of monophyletic groups, it also frees the term "species" to represent some other, entirely different category. And, if freed in this way, why not use the term to designate some kind of interbreeding group?

A Disjunctive Species Concept

An alternative to species concepts based on interbreeding as well as those based on common descent is to base the concept on both of these processes—a disjunctive definition of the species category (cf. Hull, 1965; Løvtrup, 1987). Under such a concept, species *either* would be populations (whether monophyletic or not), *or* they would be monophyletic (but not para- or polyphyletic) groups of populations. This alternative allows all populations/organisms to be assigned to species level taxa. It has other implications as well. First, to the extent that only populations are recognized as species in sexually reproducing groups, it converges on the approach of recognizing every separate population as a species. Second, some "species" would be different kinds of entities than other "species" as well as taxa at other levels in the phylogenetic system. From the viewpoint of cladistic analysis these considerations may seem unimportant, because both populations and monophyletic groups are appropriate terminal taxa. In any case, this problem could be remedied by introducing a new set of conventions (along the lines of "metaspecies") to distinguish these different kinds of entities from one another. However, in view of the confusion that might be generated by mixing the processes of interbreeding and common descent, a disjunctive definition may create more problems than it solves, especially if its only benefit is maintaining the tradition of assigning all populations/organisms to taxa of the species category.

Conclusions

Our analysis implies that neither populations nor monophyletic groups are generally more real or significant than the other; instead, their relative significance varies with the particular theoretical context. We therefore agree with the tenet that "there is no unique relation which is privileged in that the species taxa it generates will answer to the needs of all biologists and will be applicable to all organisms" (Kitcher, 1984: 309). Nevertheless, we reject the brand of pluralism that applies different criteria or even different combinations of criteria on a case by case (group by group) basis in an attempt to achieve a single, optimal, general-purpose taxonomy. Attempting to reflect a combination of processes so as to provide species taxa significant in all contexts will only result in confusion over what species taxa represent and how they might be used.

From the viewpoint of phylogenetic systematics, each of the species concepts we have considered designates units that can be used as terminal taxa, and each one also has consequences. Disjunctive species concepts, because they mix different classes of systems, result in species taxa that are not comparable. Such concepts are at odds with the unambiguous representation of different kinds of systems. Species concepts based on interbreeding entail the absence of species in organisms that reproduce only asexually. Within this category of species concepts, potentially interbreeding groups of organisms may be neither monophyletic nor cohesive, that is, they may not represent unitary evolutionary entities, and they may exhibit cladistic relationships among their included populations. Species concepts based on actual interbreeding may result in recognizing as separate "species" entities that over longer time periods function together as a single evolutionary unit. Finally, if all species are to be monophyletic, then some organisms are not parts of species, although in contrast with species concepts based on interbreeding, these organisms are not asexuals but members of ancestral populations.

In considering these consequences, a given reader may see some as insurmountable difficulties and others as simple facts of life. However, which consequences are viewed as problems and which ones as facts will differ depending on one's point of view. This is the species problem. Given this state of affairs, we can imagine several possible fates for the term "species". One possibility is that it may become restricted to one of the classes of real biological entities, such as those resulting from interbreeding or those resulting from common descent. Which of these concepts is favored depends not only on the theoretical context but also on whether "species" is viewed as the name of a class of real biological entities or as the name of a rank in a hierarchy within a class of real biological entities. Alternatively, "species" may continue to be used as a general term referring to an assemblage of several classes sharing nothing more than having been conflated historically. Realistically, the use of the term "species" will be determined as much by historical and sociological factors as by logic and biological considerations. In any case, the entities deriving their existence from different natural process are all valid objects of investigation. Acknowledging this fact and exploring the relations among the different kinds of entities is central to both biology and systematics.

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