Phylogeny as a Central Principle in Taxonomy: Phylogenetic Definitions of Taxon Names

Kevin de Queiroz, Jacques Gauthier

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PHYLOGENY AS A CENTRAL PRINCIPLE IN TAXONOMY: PHYLOGENETIC DEFINITIONS OF TAXON NAMES

KEVIN DE QUEIROZ AND JACQUES GAUTHIER

Department of Herpetology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

Abstract.—Defining the names of taxa in terms of common ancestry, that is, using phylogenetic definitions of taxon names, departs from a tradition of character-based definitions by granting the concept of evolution a central role in taxonomy. Phylogenetic definitions bear on other taxonomic principles and practices, including the following: (1) Names cannot be applied to nonmonophyletic taxa as the result of mistaken ideas about relationships or characters. Such mistakes do not affect conclusions about the monophyly of taxa but about their content and/or diagnoses. Because nonmonophyletic taxa can only be named deliberately, they are easily avoided. (2) Definitions are clearly distinguished from descriptions and diagnoses. Definitions are ontological statements about the existence of entities that result from the relationships of common ancestry among their parts; descriptions and diagnoses are epistemological statements about how we recognize the parts of those entities. (3) By precisely specifying the clade (ancestor) with which a name is associated, phylogenetic definitions clarify the limits of taxa, and this in turn clarifies related phenomena such as time of origin and duration. (4) Unlike the case for character-based intensional definitions and enumerative extensional definitions, phylogenetic definitions provide an unambiguous criterion for synonymy of taxon names: names are synonymous if they refer to clades stemming from the same ancestor. (5) Because of their relevance to synonymy, phylogenetic definitions also are relevant to priority, of both names and authorship. In phylogenetic taxonomy, priority is based not on first use of a name at a particular rank or rank-group but on first use of a name in association with a particular ancestor. [Definition; diagnosis; nomenclature; phylogeny; priority; synonymy; taxonomy.]

> Such expressions as that famous one of Linnaeus, and which we often meet with in a more or less concealed form, that the characters do not make the genus, but that the genus gives the characters, seem to imply that something more is included in our classification, than mere resemblance. I believe that something more is included; and that propinquity of descent . . . is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications [Darwin, 1859: 413–414].

Despite the widespread belief that modern biological taxonomy is based on our knowledge of evolutionary history, the development of phylogenetic taxonomy remains incomplete. As the principle of common descent gained acceptance, it took on a superficial rather than central role in taxonomy. Preexisting taxonomies came to be interpreted as the result of evolution, and evolutionary principles were developed to justify long-standing taxonomic practices, but the principle of descent did not become a central tenet from which taxonomic principles and methods were derived (Stevens, 1984; de Queiroz, 1988).

In several important respects, the concept of evolution retains this superficial rather than central role. The definitions of the names of taxa is one area in which the concept of evolution has yet to be granted a central role—a change that would have important taxonomic consequences. Although the possibility of phylogenetic definitions of taxon names, that is, definitions based on phylogenetic relationships, has been suggested (e.g., Wiley, 1979, 1989; Ghiselin, 1984; Ridley, 1986; Rowe, 1987; de Queiroz, 1988; Gauthier et al., 1988a), the significance and consequences of adopting this kind of definition have not received a detailed treatment. Here we explore the history of the definitions of taxon names, the fundamental role that definitions based on ancestry play in phylogenetic taxonomy, and some of the consequences of adopting such definitions.

"Phylogenetic taxonomy," as we use this term, is concerned with the representation of phylogenetic relationships, specifically, with issues related directly to the naming of taxa and not with those concerning how relationships are determined. Consequently, we assume the goal of representing phylogenetic relationships as well as some of the basic principles of the more inclusive discipline called "phylogenetic systematics," for example, the principle of synapomorphy and the untenability of paraphyletic taxa. The logical bases of these propositions have been considered thoroughly elsewhere (e.g., Hennig, 1965, 1966, 1975; Brundin, 1966; Nelson, 1971, 1974; Rosen, 1974; Platnick, 1978; Eldredge and Cracraft, 1980; Wiley, 1981; Ax, 1987; de Queiroz, 1988). Because we are concerned with the naming of systems of common descent, we avoid the term "classification," which is best restricted to the recognition of classes (Griffiths, 1974; Hennig, 1975; Ax, 1987; de Queiroz, 1988).

Our discussion of phylogenetic taxonomy concerns the so-called higher taxa, which, in phylogenetic systematics, are named clades or monophyletic entities (e.g., Hennig, 1966), that is, biological systems deriving their existence from the process of common descent (Griffiths, 1974; Hennig, 1975; Ax, 1987; de Queiroz, 1988). The relevance of our discussion to taxa of the species category depends on whether one's species concept refers to a subgroup of the category "clades," in which case the arguments presented here apply to species, or if it refers to the class of biological systems deriving their existence from the process of interbreeding, in which case these arguments do not apply to species (see de Queiroz and Donoghue, 1988). Finally, we discuss the definitions of taxon *names*. Definitions are given to words, including names, not to the things that the names represent, that is, the taxa themselves (Ghiselin, 1966a). Because previous authors seldom distinguished between taxa and their names, they effectively treated definitions as if they applied to both.

THE HISTORY OF DEFINITIONS OF TAXON NAMES

Aristotelian Definitions

According to Hull (1965:315), ". . . in no other science is definition as important as it is in taxonomy." In this light, it is surprising that the way in which the names of taxa are defined has changed little over the last 2,000 years. It also exemplifies the failure of the theory of evolution to penetrate the core of biological taxonomy. Although other forms of definition have been suggested, traditionally, taxon names have been treated as if they are defined by characters possessed by those organisms considered to be members of the taxa. Under such character-based definitions, taxa have been treated as if they are classes of organisms (Ghiselin, 1969, 1974; Hull, 1976, 1978; de Queiroz, 1988; for explicit examples see Gregg, 1950; Beckner, 1959; Buck and Hull, 1966, 1969; Muir, 1968; Suppe, 1974, 1989) in that their characters have been viewed as intensions, that is, those properties connoted by the taxon names. Consequently, traditional definitions of taxon names have been considered intensional definitions (e.g., Ruse, 1973). Such definitions have their roots in the Aristotelian form of definition, which was summarized by Hull as follows:

> In Aristotle's view three things can be known about any entity—its essence, its definition, and its name. The name names the essence. The definition gives a complete and exhaustive description of the essence. Derivatively, the name is the name of the entity and the definition a description of it [Hull, 1965:318].

Most modern taxonomists have abandoned the notion of essences (but see Kitts, 1983; Bernier, 1984), and many have rejected the notion that taxa are classes of organisms. Nevertheless, elements of the Aristotelian form of definition have persisted in modern biological taxonomy in that the names of taxa continue to be treated as if they are defined by lists of organismal characters (see the section titled "Definition" in numerous recent taxonomic papers).

Cluster Concepts: Character-Based Definitions that Accommodated Evolution

In post-Darwinian times it has become accepted widely that biological taxonomy is, or should be, evolutionary. However, even disassociated from the notion of essences, the Aristotelian form of definition proved to be incompatible with the principle of evolution (Hull, 1965). As Hull (1965:318) noted, "... what Aristotle was advocating in modern terms is definition by properties connected conjunctively which are severally necessary and jointly sufficient [for membership in the taxon]." But evolutionary change may result in loss or modification, in lineages within a taxon, of the very characters that supposedly define the name of that taxon. Given that the modified lineages remain parts of the taxon, it must be concluded that the characters in question were not necessary and sufficient to define its name (Sober, 1988; see also Beatty, 1982).

Hull (1965) noted that names can be defined by kinds of (intensional) definitions other than conjunctive ones, that is, definitions in which each property in the entire set is necessary for membership (e.g., a bachelor is both unmarried and male). For example, names also can be defined disjunctively, that is, by sets of properties not all of which are necessary, without violating the spirit of Aristotelian definition. Thus, each property in a definite disjunctive definition may be sufficient by itself, and only some subset of the properties is necessary for group membership (e.g., a sibling is either a brother or a sister). Hull (1965:323; see also Beckner, 1959; Hull, 1974) argued, however, that "... neither of these types of definition is appropriate for defining the names of taxa and, hence, for delineating taxa. Whether from the viewpoint of phylogenetic or numerical taxonomy, taxon names can be defined only *by sets of statistically covarying properties arranged in indefinitely long disjunctive definitions*" (emphasis in original). The distinction between definite conjunctive definitions and indefinite disjunctive definitions was also made by Beckner (1959) and by Sneath (1962), who used the terms "monothetic" and "polythetic" to refer to the classes of taxa based on these two classes of definitions.

Indefinite disjunctive definitions, or cluster concepts, avoided the problem that evolution posed for Aristotelian definitions. Because no character or set of characters was necessary for the definition of a taxon name, and any one of numerous sets was sufficient, evolutionary change could occur without invalidating the definition. Nevertheless, cluster concepts, like Aristotelian definitions, defined taxon names in terms of characters. Although such definitions may have been consistent with evolution, they were not evolutionary, which is to say that they made no reference to common descent or any other evolutionary phenomenon.

Phylogenetic Definitions

Taxonomists have long suspected that the characters of taxa are merely manifestations of a more fundamental phenomenon (see epigraph). But despite the fact that most taxonomists subsequent to Darwin have accepted evolution as that underlying phenomenon, they are only beginning to realize that this concept provides the possibility of an entirely different kind of definition.

Viewing taxa as wholes, or individuals, led Ghiselin (1966b, 1974, 1981, 1984) and Hull (1976, who rejected his earlier treatment of taxa as classes) to conclude that the names of taxa are proper names and hence can only be defined ostensively, that is, by pointing out the entity to which the name is given. A simple enumeration of included subtaxa (pointing out the members or representatives) does not qualify as an evolutionary ostensive definition, for it makes no reference to evolution. Furthermore, if enumeration is viewed as listing a taxon's known content with an implicit statement about common ancestry, it fails to capture the intended meaning of the name. Simple enumeration makes no provision for the discovery of previously unknown representatives of a taxon. In order to make the definitions of taxon names evolutionary, they must be rooted in the concept of common ancestry. Thus, an evolutionary ostensive definition, hereafter referred to as a phylogenetic definition, consists of pointing to a clade, that is, to an ancestor and its descendants (Ghiselin, 1984). This can be accomplished, verbally or on a

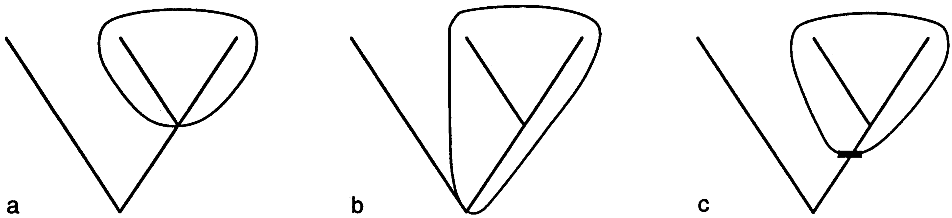

FIG. 1. Three possible ways of defining taxon names phylogenetically. (a) Node-based definition. (b) Stem-based definition. (c) Apomorphy-based definition (bar indicates origin of the apomorphy). See text for explanations and examples.

branching diagram, in at least three different ways:

1. By defining the name of a taxon as the clade stemming from the most recent common ancestor of two other taxa, hereafter referred to as a *node-based definition* (Fig. 1a). For example, Gauthier et al. (1988a:34) defined "Lepidosauria" as "the most recent common ancestor of *Sphenodon* and squamates and all of its descendants." (For other examples see de Queiroz [1987], Estes et al. [1988], Gauthier et al. [1988a, b], and Rowe [1988].)

2. By defining the name of a taxon as all those entities sharing a more recent common ancestor with one recognized taxon than with another, hereafter referred to as a *stem-based definition* (Fig. 1b). For example, Gauthier et al. (1988a:27) defined "Lepidosauromorpha" as "*Sphenodon* and squamates [Lepidosauria] and all saurians sharing a more recent common ancestor with them than . . . with crocodiles and birds." (For other examples see Gauthier et al. [1988a, b].)

3. By defining the name of a taxon as the clade stemming from the first ancestor to possess a particular synapomorphy, hereafter referred to as an *apomorphy-based definition* (Fig. 1c). For example, "Tetrapoda" is usually defined implicitly as the first vertebrate to possess digits (i.e., hands and feet rather than fins) and all of its descendants.

All three classes of phylogenetic definitions are firmly rooted in the concept of common ancestry in that this concept is fundamental to the meaning of taxon names. Although the apomorphy-based phylogenetic definition makes reference to a character, it differs fundamentally from a character-based intensional definition. In contrast with the latter, the character used in an apomorphy-based phylogenetic definition is simply a means of specifying an ancestor. The definition does not imply the presence of the character in all organisms of the taxon, for these characters may be lost in some descendants of the specified ancestor. Thus, it is neither necessary nor sufficient for an organism to possess the character in order to be considered part of the taxon; what is both necessary and sufficient is being descended from the specified ancestor.

The use of phylogenetic definitions liberates biological taxonomy from a 2,000-year-old tradition of basing the definitions of taxon names on characters. Because of the antiquity of this tradition and the importance of definitions in taxonomy (Hull, 1965), one might expect the adoption of phylogenetic definitions to have far-reaching consequences for other taxonomic principles, practices, and conventions.

PROPERTIES OF PHYLOGENETIC DEFINITIONS

Relationship to the Concepts of Monophyly, Paraphyly, and Polyphyly

Traditional definitions of taxon names take the same form, that is, lists of characters, regardless of whether the taxa are monophyletic, paraphyletic, or polyphyletic. Although the definitions of these three classes of taxa are stated in terms of common ancestry (e.g., Hennig, 1966; Farris, 1974), the classes themselves are nevertheless characterized by different classes of characters: synapomorphies in the case of monophyletic taxa, symplesiomorphies in the case of paraphyletic taxa, and convergences in the case of polyphyletic taxa (Hennig, 1965, 1966, 1975). For any given taxon, however, both the patterns of common ancestry that would place it in one of the three classes of taxa and the apomorphic, plesiomorphic, or homoplastic status of its characters can be recognized only in the context of an accepted phylogeny. Consequently, under character-based definitions of taxon names, nonmonophyletic taxa can be named accidentally. If phylogenetic relationships are unknown (the synapomorphic, symplesiomorphic, or homoplastic status of the characters is ignored or uncertain) or if notions of phylogenetic relationships are in error (symplesiomorphies or homoplasies are mistaken for synapomorphies), then paraphyletic or polyphyletic taxa can be named accidentally even by those wishing to avoid them.

Under phylogenetic definitions, names will never be defined as referring to nonmonophyletic taxa as the result of mistakes; the associations must be deliberate, and this holds regardless of potential mistakes about phylogenetic relationships (see below). Consequently, the very definitions of their names give warning of paraphyletic and polyphyletic taxa. The names of paraphyletic taxa must be defined as monophyletic taxa from which a part or parts have been removed, that is, as incomplete systems of common ancestry. For example, "Reptilia," traditionally the name of a paraphyletic taxon, might be defined as "the most recent common ancestor of Mammalia and Aves and all of its descendants *except* Mammalia and Aves." On the other hand, the names of polyphyletic taxa must be defined as sets of two or more separate systems of common ancestry. For example, "Haemothermia," the name of a diphyletic taxon, might be defined as "the most recent common ancestor of monotremes and therians and its descendants (=Mammalia) *and* the most recent common ancestor of paleognaths and neognaths and its descendants (=Aves)." The incomplete nature of paraphyletic taxa and the composite nature of polyphyletic taxa are thus revealed directly by the manner in which their names are defined. In contrast, definitions of the names of monophyletic taxa contain no phrases excluding certain descendants of the specified common ancestor from the taxon, nor do they require conjunctions linking separate systems of common ancestry.

The relevance of these considerations to phylogenetic taxonomy is that because names can only be associated with nonmonophyletic taxa deliberately, such associations are easily avoided. Furthermore, phylogenetic definitions can be worded so that they *necessarily refer only to monophyletic entities*. This does not mean that mistakes cannot be made; however, such mistakes will be seen for what they are, that is, mistakes about phylogenetic relationships, diagnostic characters, or included taxa. They will never result in the conclusion that a name originally defined as referring to a monophyletic taxon actually refers to a paraphyletic or polyphyletic group.

For example, Gauthier et al. (1988a) defined the name "Lepidosauromorpha" as all saurians sharing a more recent common ancestor with lepidosaurs than with archosaurs. They considered Lepidosauromorpha to include lepidosaurs, kuehneosaurs, *Paliguana**, *Saurosternon**, *Palaeagama**, and Younginiformes, as illustrated in Figure 2a (an asterisk after a taxon name indicates that evidence for monophyly is lacking). Now suppose that the true phylogenetic relationships of Younginiformes are as illustrated in Figure 2b; this taxon is the sister group of the clade stemming from the most recent common ancestor of Lepidosauria and Archosauria. Under traditional definitions of taxon names, one might conclude that Lepidosauromorpha is paraphyletic, because it now appears that Archosauria is descended from the most recent common ancestor of the taxa originally considered to be lepidosauromorphs (Fig. 2b). But according to the phylogenetic definition as stated, this is not so. The definition of "Lepidosauromorpha" does not contain a phrase excluding any descen-

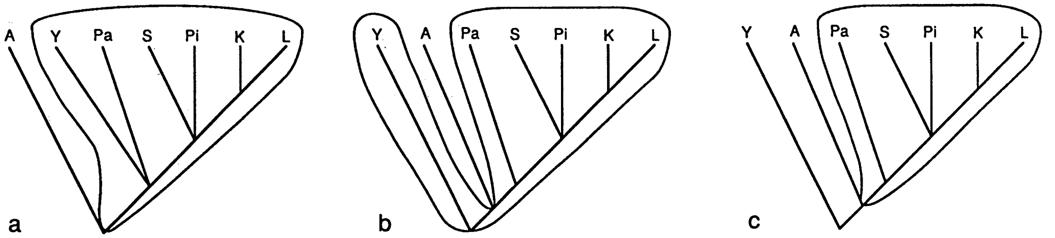

FIG. 2. Phylogenetic definitions and monophyly. (a) Phylogenetic relationships within Sauria, with bubble encircling Lepidosauromorpha as its name was defined by Gauthier et al. (1988a). (b) Hypothetical change in ideas about the relationships of Younginiformes (Y), which seems to imply paraphyly of Lepidosauromorpha when the content rather than the definition is considered. (c) The actual limits and monophyly of Lepidosauromorpha under the revised relationships according to the definition as stated. See text for additional discussion. *Abbreviations:* A, Archosauria; Y, Younginiformes; Pa, *Palaeagama**; S, *Saurosternon**; Pi, *Paliguana**; K, Kuehneosauridae; L, Lepidosauria.

dants of the specified common ancestors; therefore, this name *must* refer to a monophyletic taxon. And, because it is defined with respect to Archosauria, one must conclude *not* that Lepidosauromorpha is paraphyletic, but that Younginiformes is not part of it (Fig. 2c).

By granting the principle of descent a central role in biological taxonomy, phylogenetic definitions reorient questions away from the monophyletic, paraphyletic, or polyphyletic status of taxa to their content and diagnoses. The concepts of monophyly, paraphyly, and polyphyly were formulated in an era when the evolutionary world view had been accepted but was granted the role of little more than an after-the-fact interpretation of the order already manifest in taxa (see de Queiroz, 1988). Largely as a result of Hennig's writings (e.g., 1965, 1966, 1975), the role of the concept of evolution in biological taxonomy began to change—from that of a superficial interpretation to that of a central tenet (de Queiroz and Donoghue, 1988, 1990). But Hennig did not take this perspective to its logical conclusion, that is, adopting phylogenetic definitions of taxon names and stating these definitions in such a way that all taxa necessarily would be monophyletic. And because taxon names have continued to be defined with respect to characters rather than ancestry, it was meaningful not only for Hennig, but also for systematics up to the present time, to inquire about whether these names referred to monophyletic entities.

The use of phylogenetic definitions will effectively initiate a new era in biological taxonomy. In this era there will be, in one sense, no existing taxa (named entities), for the names have not yet been tied explicitly to the entities through phylogenetic definitions. Once these names are tied to the entities by their definitions as complete systems of common ancestry, all taxon names can be worded so that they refer to monophyletic entities *by definition.* Consequently, the concepts of paraphyly and polyphyly will become superfluous and interesting primarily in a historical context. The significant question no longer will be whether a taxon is monophyletic, paraphyletic, or polyphyletic; instead (as in the example of Lepidosauromorpha, above) the significant questions about any taxon will concern its content and its diagnostic characters (see below).

As one manifestation of granting the principle of descent the role of a central tenet in taxonomy, phylogenetic definitions acknowledge that common ancestry is fundamental to the existence of the things being named. Accepting this proposition provides the basis for stable and unambiguous phylogenetic meanings of taxon names in the context of changing ideas about the details of phylogeny, both in terms of relationships and in terms of the precise level at which particular characters exist as synapomorphies. This stability and clarity derives from the fact that, for any two organisms, common ancestry at *some* level is certain, whereas the precise content of a taxon and its diagnostic characters are not.

Metataxa

The relevance of phylogenetic definitions to metataxa—taxa based on plesiomorphy but for which evidence of paraphyly, and monophyly, is lacking (Donoghue, 1985; Gauthier et al., 1988a)—is similar to that concerning paraphyletic and polyphyletic taxa. Although it is possible to define the name of a metataxon phylogenetically, there would be little reason for doing so. Metataxa require uncertainty about relationships of common descent, and, therefore, the phylogenetic definitions of their names require ambiguous statements about these relationships. Using a phylogenetic definition, the name of a metataxon must be defined as a common ancestor and all, or maybe only some, of its descendants. Like the concepts of paraphyly and polyphyly, the metataxon concept is the product of an era in which phylogenetic relationships had become important considerations, but characters, rather than phylogenetic relationships, continued to be granted primacy in the definitions of taxon names. Indeed, the very fact that paraphyly, polyphyly, and metataxa are important concepts is evidence that taxon names continue to be treated as if they are defined by characters rather than by phylogenetic relationships. If the use of phylogenetic definitions becomes predominant, then the metataxon concept, like those of paraphyly and polyphyly, will become superfluous except in a historical context.

Relationship to Characters

Some properties of phylogenetic definitions are clarified by considering their relationship to characters. It is sometimes said that characters are diagnostic (or descriptive) of taxa rather than defining (e.g., Ghiselin, 1966a, b, 1984, 1985; Hull, 1976; Wiley, 1979; Beatty, 1982; Ridley, 1986; Sober, 1988). The difference between definition and diagnosis is that between an entity itself and the evidence for its existence, that is, between ontology and epistemology. This distinction is obscured by traditional definitions of taxon names, because traditional definitions take the same form as descriptions and diagnoses, that is, lists of characters (Ghiselin, 1966a). From an essentialist's perspective, character-based intensional definitions make ontological (as well as epistemological) statements in that they are viewed as descriptions of a taxon's essence, and the essence is that from which the taxon derives its existence. When the essentialist underpinnings are removed, however, character-based definitions confuse ontology and epistemology. The taxon seems to exist solely because its organisms have characters by which we recognize them as belonging to the taxon.

Adopting phylogenetic definitions clarifies the distinction between definition and diagnosis. Here the definitions of taxon names are ontological statements in that they refer to monophyletic entities (clades), which are presumed to exist under the central tenet of common descent independent of our ability to recognize them. Monophyletic taxa, that is, named clades, are not concepts (contra Løvtrup, 1986) but real things—systems deriving their existence from common ancestry relationships among their parts (Griffiths, 1974; Hennig, 1975; de Queiroz, 1988). Phylogenetic definitions are of little use, however, unless the critical relationships can be determined. This is one role of characters. And after the relationships have been established and the taxon names defined, characters also permit the determination of which entities fit a definition, that is, whether a given specimen is a representative of the taxon in question (see Hull, 1976). Just as symptoms are used to diagnose a disease (which often has an unseen underlying cause), so characters are used to diagnose taxa (Ghiselin, 1984).

Thus, in the previous example, the change in ideas about the relationships of Younginiformes does not change the definition of "Lepidosauromorpha" or its monophyletic status. It does, however, imply changes in ideas not only about included taxa but also about diagnostic characters. One possibility is that the characters formerly thought to support a closer relationship of Younginiformes to Lepidosauria than to Archosauria actually diagnose a more inclusive taxon of which Archosauria is a part. Perhaps derived characters formerly thought to be absent in archosaurs are determined to be present in a modified form. In this case the characters in question turn out to be irrelevant to determining which entities fit the definition of the name "Lepidosauromorpha." This name is defined as all saurians sharing a more recent common ancestor with Lepidosauria than with Archosauria, even if the characters thought to be diagnostic of this taxon actually apply to a more inclusive clade.

Alternatively, the conclusion that certain derived characters are diagnostic of Lepidosauromorpha may remain unchanged, but now it is concluded that younginiforms do not possess these characters. Younginiforms are extinct, and the characters in question may have involved poorly preserved parts of the body. Perhaps new specimens or further preparation has revealed that the characters once thought to be present are in fact absent.

A strength of viewing characters as diagnostic rather than defining of taxon names is that it avoids certain problems for the traditional form of definition caused by plesiomorphy and homoplasy. How can Tetrapoda, for example, be defined by the presence of limbs if some tetrapods (e.g., snakes) lack them? One possibility is to use cluster concepts in which none of the defining characters is necessary for taxon membership. Another possibility is to consider the absence of limbs to be a modified form of the character "limbs present" (e.g., Platnick, 1979). The solution is simpler and more straightforward under phylogenetic definitions. Here the absence of limbs in snakes in no way compromises the name Tetrapoda, defined as the clade stemming from a particular limbed ancestor. Because snakes are among the descendants of this ancestor, they are tetrapods whether they have limbs or not. The absence of limbs in snakes only makes it more difficult to establish their tetrapod ancestry.

Relationship to Taxon Limits and Origination Times

By precisely specifying the clade (ancestor) to which a name refers, phylogenetic definitions clarify ambiguities about the limits of taxa that are perpetuated under traditional, character-based definitions. One of these concerns the discovery of new taxa. Under the traditional form of definition, it was generally considered preferable to base the definition of a taxon name on several characters, presumably because having more characters constitutes better support for that taxon. However, the discovery of organisms possessing some but not all of the defining characters of a taxon posed problems. Are these organisms part of that taxon? Are all of the characters defining, or only some of them, and if the latter, which ones? Thus, for example, the discovery of monotremes led to a debate about whether these animals were mammals or representatives of some separate taxon (Gould, 1985). That this debate occurred implies that the limits and hence the defining characters of "Mammalia" were called into question. Similar problems continue to the present day, especially in paleontology where organisms with new combinations of characters are discovered regularly (see Rowe, 1988).

Phylogenetic definitions in no way diminish the significance of such intermediate forms, but they focus attention away from purely definitional issues to phylogenetic ones. For example, in the case of *Archaeopteryx*, the interesting issue is not whether these fossils truly can be called birds; rather, it is their phylogenetic relationships. Given that these relationships have been determined, then the question of whether *Archaeopteryx* is a bird depends entirely on how "bird" is defined (e.g., Thulborn, 1984; Gauthier, 1986). Thus, if *Archaeopteryx* is the sister group of all other known feathered vertebrates and "birds" is defined as the most recent common ancestor of paleognaths and neognaths and its descendants, then *Archaeopteryx* is not a bird. But, if "bird" is defined as the first feathered vertebrate and its descendants or as all archosaurs sharing a more recent common ancestor with extant birds than with crocodylians, then *Archaeopteryx* is a bird. And although it may be more traditional, convenient, or useful to adopt one of the various possible definitions of "bird" and hence settle the issue of whether *Archaeopteryx* is or is not part of this taxon, the choice is a definitional rather than a biological issue.

Because phylogenetic definitions precisely specify the limits of taxa, they also clarify questions about times of origin and consequently about temporal durations, both of which are susceptible to confusion under traditional definitions (Rowe, 1988). Under character-based definitions, discrepancies in the ages assigned to a taxon can result, even in the absence of conflicting data, from inconspicuous differences in the definition of the name. What appears to be the same taxon as judged by its name and many, perhaps most, of its "defining" characters, may in fact be two different taxa in terms of the common ancestors implied by slightly different sets of characters. For example, Mammalia of some authors is based solely on the character dentary–squamosal articulation between cranium and mandible, whereas other authors base a taxon of the same name on this and additional characters (Rowe, 1988). Given that some of the additional characters arose before or after the dentary–squamosal articulation, as indeed it apears they did (Rowe, 1988), then the name "Mammalia" does not always refer to the same clade (Fig. 3). Because these different clades form a nested series, their ages must differ. Therefore, estimates of the age of Mammalia may differ given the same hypothesized relationships and known fossils simply because certain fossils will be considered mammals according to some definitions of "Mammalia" but not others.

The general problem described above was recognized by Hennig (1965, 1981; see also Jefferies, 1979; Lauterbach, 1989). Indeed, three different meanings of a taxon's time of origin recognized by Hennig represent special cases of the three classes of phylogenetic definitions identified in this paper. These are (1) the time at which certain lineages represented by extant organisms last shared a common ancestor (Hennig's * group, Jefferies's crown group, Lauterbach's monophylum sensu stricto; a special case of the node-based definition), (2) the time at which the stem lineage of that clade separated from its sister group (Jefferies's total group, Lauterbach's panmonophylum; a special case of the stem-based definition), and (3) the time at which the "typical" characters of the extant representatives of the clade arose in its stem lineage (a special case of the apomorphy-based definition). A given name could be defined in any of these three ways, but each would refer to a different ancestor and, therefore, to a more or less inclusive clade. This fact has important consequences for various time-related phenomena, such as estimates of the origination times and durations of taxa and the calibration of molecular clocks.

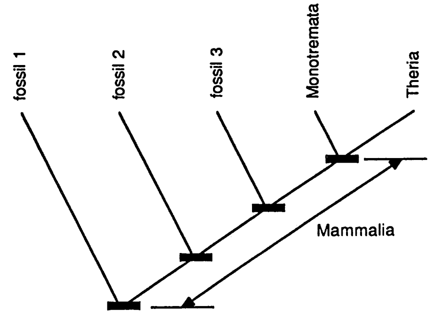

FIG. 3. Ambiguities in the boundaries of taxa under character-based definitions of taxon names. If different authors define the name "Mammalia" with respect to different sets of the characters (indicated by bars in diagram), then "Mammalia" will refer to different clades, some more inclusive than others. Therefore, the three fossils will be mammals according to some definitions but not according to others.

Phylogenetic definitions avoid such ambiguities concerning the limits of taxa, because the ancestors in question are clearly specified. This is not to say that different authors cannot use the same name to refer to different clades. However, phylogenetic definitions of the same name as used by different authors should reveal whether that name refers to the same or to different

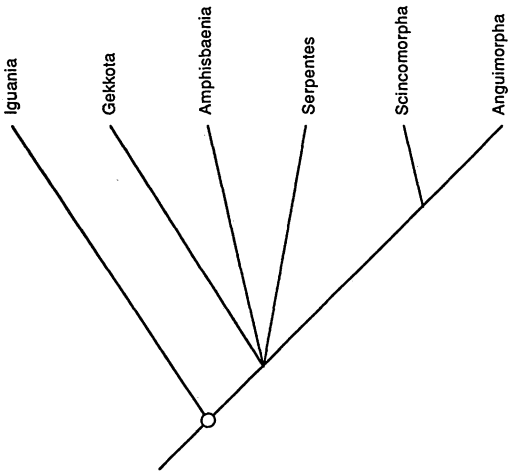

FIG. 4. Synonymy under phylogenetic definitions. "Lacertilia" (defined as the clade stemming from the most recent common ancestor of Iguania, Gekkota, Scincomorpha, and Anguimorpha) and "Squamata" (defined as the clade stemming from the most recent common ancestor of Lacertilia, Serpentes, and Amphisbaenia) refer to the same ancestor (circle) if the relationships among these taxa are as illustrated. Therefore, "Lacertilia" and "Squamata" are synonymous.

ancestors, and if they do not, this suggests possible disagreements concerning phylogenetic relationships (see Synonymy, below).

Synonymy

The issue of taxonomic synonymy, whether different names refer to the same entity, is clarified by phylogenetic definitions. Under character-based and enumerative definitions, synonymy often is a matter of degree. When the definitions of different names are identical in terms of characters and included taxa, then synonymy seems obvious, but how closely must they correspond if they are not identical? And what criteria are to be used in deciding this issue? Under traditional definitions of taxon names, the answers to these questions are not straightforward. In contrast, phylogenetic definitions provide a nonarbitrary and unambiguous criterion for synonymy: names are synonymous if and only if they refer to clades stemming from the same ancestor.

For example, suppose that (1) "Squamata" is defined as the most recent common ancestor of Lacertilia, Serpentes, and Amphisbaenia, and its descendants; (2) "Lacertilia" is defined as the most recent common ancestor of Iguania, Gekkota, Scincomorpha, and Anguimorpha, and its descendants; and (3) the relationships among these taxa are as shown in Figure 4 (Estes et al., 1988). Without considering phylogenetic relationships, the definitions of the two names seem to indicate that "Squamata" refers to a more inclusive clade than does "Lacertilia." This is contradicted by the phylogenetic relationships. The definitions of both "Squamata" and "Lacertilia" refer to the same ancestor—the one at the base of the diagram (Fig. 4). Therefore, given the definitions stated and the relationships illustrated, these names are synonymous. That the two names previously may have been viewed as referring to different clades is accounted for by a mistake about the content of Lacertilia, namely, that Serpentes and Amphisbaenia were thought not to be parts of it.

Of course, phylogenetic definitions can clarify issues of synonymy only in the context of relevant knowledge about phylogenetic relationships. The situation is greatly simplified by, but it is not dependent on, there being a single accepted phylogeny. Thus, in Figure 5a, the name defined as the clade stemming from the most recent common ancestor of A and D is synonymous with the name defined as the clade stemming from the most recent common ancestor of B and E, even though the relationships of C are controversial. Synonymy also would obtain if the definitions of one, the other, or both names included reference to C as one of the descendants of the specified ancestor.

Certain differences among competing phylogenetic hypotheses render questions of synonymy unresolvable. Suppose, using the previous example, that two different names are defined under the alternative phylogenetic hypotheses (Fig. 5b, c): one for the clade stemming from the most recent common ancestor of A, B, C, D, and E and the other for the clade stemming from the most recent common ancestor of A, B,

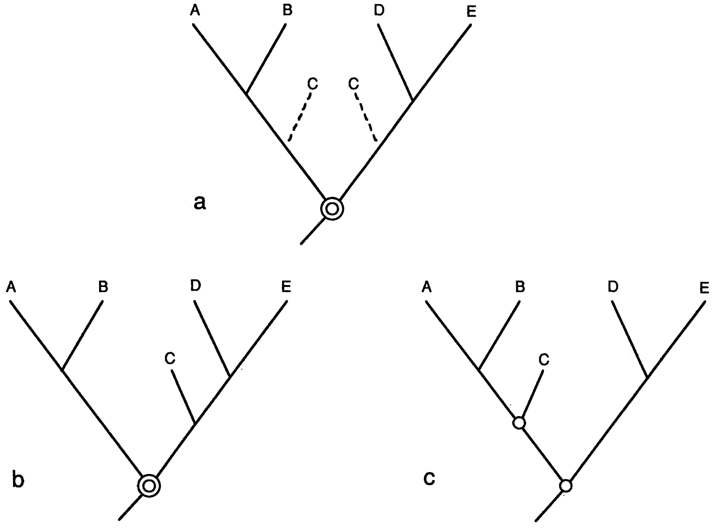

FIG. 5. Synonymy in cases of uncertain phylogenetic relationships. (a) The name of the node-based taxon stemming from the most recent common ancestor of A and D is synonymous with the name of the node-based taxon stemming from the most recent common ancestor of B and E, despite uncertainty about the relationships of C. (b, c) Names of node-based taxa defined with respect to the most recent common ancestors of A, B, C, D, and E and of A, B, and C are synonymous under one of the possible resolutions of the relationships of C (b), but not the other (c). Circles indicate ancestors specified by the definitions.

and C. According to one of the two hypotheses the names are synonymous (Fig. 5b), but according to the alternative they are not (Fig. 5c). Accepting one of these hypotheses and rejecting the other resolves the issue of synonymy, but if the relationships are considered unresolved and both hypotheses are retained, the issue of synonymy cannot be resolved. This situation should be viewed as a strength rather than a weakness of phylogenetic definitions. It emphasizes that synonymy can be resolved only in the context of the relevant phylogenetic information.

Although the implicit phylogenetic meaning of taxon names is generally clear when only extant organisms are considered, ambiguities often arise when considering fossils (e.g., Patterson and Rosen, 1977; Jefferies, 1979; Hennig, 1981; Lauterbach, 1989). For example, there is no disagreement about the content of Amniota when only extant organisms are considered. In this context, the phylogenetic definition of "Amniota" might be stated as the most recent common ancestor of Mammalia, Chelonia, Archosauria, and Lepidosauria, and its descendants (a node-based definition of the crown group). Nevertheless, the implicit meaning of "Amniota," as this name is most commonly used, is the clade stemming from the first vertebrate to possess an egg with an amnion (an apomorphy-based definition). In the extant biota, the content of Amniota under these alternative definitions is identical; however, if extinct organisms are also considered, then these two definitions may refer to different clades, one more inclusive than the other. In other words, the amniote egg may have arisen prior to the most recent common ancestor of extant amniotes. A stem-based definition of the "total" group (Jefferies, 1979) is also possible; for example, Gardiner (1982, 1983) implicitly defined "Amniota" as Recent amniotes and all organisms that are more closely related to them than to extant amphibians. Regardless of which definition of "Amniota" is favored, the different possibilities illustrate a general point: although it is usually possible to identify a series of ancestors as being implicitly associated with the name of a traditional taxon (e.g., Fig. 4), the precise ancestor in this series often will be ambiguous. Furthermore, although there exists an awareness of these distinctions, traditional practice has been to use the same name for both crown and "total" clades (e.g., Jefferies, 1979; Hennig, 1981; Lauterbach, 1989). Given the ambiguity resulting from associating the same name with clades stemming from different ancestors in a lineage, it seems preferable to give a different name to the crown clade on the one hand and the "total" clade on the other.

As can be seen from the preceding discussion, there necessarily will be ambiguities about synonymy during the transition to a system based on phylogenetic definitions. Associations of names with particular ancestors have heretofore been implicit rather than explicit, and the forms of definition currently in use often render such associations ambiguous. This situation should encourage the redefinition of taxon names in explicit phylogenetic terms; however, due consideration should be given to diverse criteria, including implicit associations with ancestors, current and historical usage, alternative names, priority (see below), and utility to the greatest number of biologists.

Priority

The consequences of phylogenetic definitions for synonymy bear on another issue, priority, which is often resolved in a phylogenetically unsatisfactory way under traditional taxonomic conventions. In the traditional system (e.g., ICZN, 1985), priority is tied to categorical ranks. This situation can lead to drastic changes in the meanings of names (i.e., the ancestors with which the names are implicitly associated) as the result of simple changes in rank. Thus, combining several taxa of the same rank into a single one requires that the oldest name is the valid one for that taxon. This practice can result in changing the ancestor with which the name is implicitly associated to that of a more inclusive clade. Similarly, partitioning a single taxon of a particular rank into several taxa at that same rank often results in restricting the original taxon's name to a less inclusive clade.

The problem of changing the clades with which names are associated is aggravated by trying to achieve a phylogenetic taxonomy within the traditional Linnean system. This results from attempts to eliminate paraphyletic taxa, which are often accompanied by changes in ranks associated with particular names in order to satisfy the convention of mandatory categories. For example, the taxa Agamidae* and Chamaeleonidae have traditionally been assigned the rank of family, and it has been suggested that Agamidae* may be paraphyletic with respect to Chamaeleonidae (Estes et al., 1988; Frost and Etheridge, 1989). If the relationships are as illustrated in Figure 6, then "Agamidae" is paraphyletic according to its traditional definition. Nevertheless, one might interpret this name as having an implicit association with ancestor A, the most recent common ancestor of its included subtaxa (u–w). "Chamaeleonidae," on the other hand, is implicitly associated with ancestor C.

Such being the case, uniting "Agamidae" and Chamaeleonidae into a single family would eliminate a paraphyletic taxon. If this is done, then according to traditional, rank-based notions of priority (e.g., ICZN, 1985), the name of the clade stemming from ancestor A will be "Chamaeleonidae," because this is the older name in the family group (Frost and Etheridge, 1989). Given the desirability of stable phylogenetic meanings of names, this action has the undesirable consequence of changing the association of a name from one clade to a more inclusive one. The name "Chamaeleonidae," which was formerly associated with the clade stemming from ancestor C, is now associated with that stemming from ancestor A, the ancestor with which "Agamidae" was formerly associated.

It might be argued that the association of "Agamidae" with ancestor A is unjustified—that it is preferable to consider "Agamidae," the name of a paraphyletic taxon, to have had no implicit phylogenetic definition. This does not, however, solve the problem of the change in the clade with which "Chamaeleonidae" is associated. Furthermore, the name "Acrodonta" (Cope, 1864) already has been used for the clade stemming from ancestor A (Estes et al., 1988). Acrodonta, however, is considered to be assigned a rank above the family level in traditional taxonomies. Therefore, "Acrodonta" would be replaced by "Chamaeleonidae," simply because the former is not a name of the family group.

From the preceding example, it can be seen that the traditional practice of determining priority according to ranks is obfuscatory from the perspective of phylogenetic taxonomy. The associations of names with particular clades change as the result of arbitrary decisions about categorical ranks, and names applied to monophyletic entities are rejected simply because they are not of the appropriate rank. Given that a rank-based concept of priority confuses the associations of names with particular clades, a phylogenetic concept of priority should not be based on ranks.

In phylogenetic taxonomy, the concept of priority should not be based on first use of a name at a given rank or group of ranks, but on first use of a name in association with a particular clade (ancestor). Thus, to continue with the same example, "Agamidae" and "Chamaeleonidae" would remain associated with the same ancestors (A and C, respectively). If the relationships are as illustrated (Fig. 6), then Chamaeleonidae would be considered a subgroup of Agamidae rather than a separate taxon of the same rank. The names are not synonymous, and the former "paraphyly" of Agamidae is seen as a mistake about its content. Alternatively, because the name "Acrodonta" has already been used for the more inclusive clade, "Agamidae," a name formerly associated with a paraphyletic group, might be abandoned in favor of "Acrodonta" (Estes et al., 1988). If the name "Acrodonta" did not exist, it might be preferable to coin a new name for this clade rather than using "Agamidae." Any one of these alternatives is reasonable from a phylogenetic perspective, because none of them changes the associations of names with particular clades (ancestors).

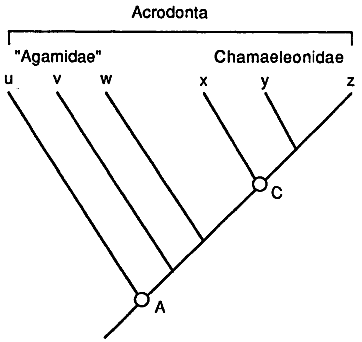

FIG. 6. Changes in the clade with which a name is associated under the traditional, rank-based criterion of priority. If "Agamidae" and Chamaeleonidae are combined into a single taxon assigned the rank of family, the name of this family is "Chamaeleonidae" because this is the older name in the family group. The result is a change in association of the name "Chamaeleonidae" from the clade stemming from ancestor C to that stemming from ancestor A.

The principle of coordination (ICZN, 1985), which deals with priority of authorship rather than of the name itself, is another nomenclatural rule that settles issues of priority in a phylogenetically unsatisfactory way. According to the principle of coordination, all names in a given rank-based group (e.g., genus group, family group) are credited to the first author to use *any* name in the group based on the same nomenclatural type. Thus, although Cope (1886) coined the name "Iguaninae" for a particular taxon of squamate reptiles, his insight is credited to Bell (1825) merely because Bell coined "Iguanidae" and both names belong to the family group (de Queiroz, 1987). This rule would be unproblematical if it applied only to situations in which the differences in the names involved only differences in categorical ranks and their associated suffixes, for example, if the family Iguanidae had been lowered in its entirety to subfamily rank. The rule applies, however, even if the names refer to different entities, for example, when "Iguanidae" refers to a more inclusive taxon than does "Iguaninae." From the viewpoint of conveying an author's association of a name with a particular taxon, this rule confuses matters, whether in phylogenetic or in Linnean taxonomy. It reflects an overemphasis on categorical ranks. As in the case of priority, authorship in phylogenetic taxonomy should not be based on the first use of a name in a particular rank-based group, but on implicit or explicit association of a name with a particular clade (ancestor).

CONCLUSION

Since Hennig's (e.g., 1965, 1966) influential writings and their popularization, phylogenetic systematics has enjoyed considerable success and made great progress. In contrast, phylogenetic taxonomy, that branch of systematics concerned with representing the relationships uncovered by phylogenetic analysis, has lagged behind. The development of phylogenetic taxonomy has been hindered in part by the implicit or explicit assumption that it is to be achieved within the traditional Linnean framework. This assumption is one example of a general phenomenon in which existing taxonomic practices are taken for granted and the evolutionary world view is overlaid upon them as a superficial interpretation. But if the Darwinian Revolution is ever to occur in biological taxonomy (Patterson, 1978; de Queiroz, 1988; O'Hara, 1988), then the role of the principle of descent must change. It must change from an after-the-fact interpretation to a central tenet from which the principles and methods of taxonomy are deduced. The principle of phylogenetic definitions exemplifies this change. Previously, taxa were considered to be defined by characters and only interpreted after-the-fact as products of evolution. Under the principle of phylogenetic definitions, evolutionary considerations enter directly into the definitions of their names. Just as the concept of synapomorphy granted the principle of common descent a central role in systematic analysis, so the concept of phylogenetic definitions grants this concept a central role in taxonomy.

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