# PHYLOGENETIC METHODS AND THE EARLY HISTORY OF AMNIOTES

In a recent review of early amniote evolution, Carroll (1982) criticized the methods of phylogenetic (cladistic, Hennigian) systematics. Specifically, he concluded that several of the most important assumptions of this methodology were contradicted by the evidence from early amniotes and that these contradictions resulted from the evolutionary process of adaptive radiation in this group. Our opinions concerning the utility of the phylogenetic method contrast strongly with those of Dr. Carroll. We feel that the problems he encountered result from his misunderstanding of the phylogenetic method rather than from inadequacies of this method itself. Dr. Carroll is one of the most knowledgable students of early amniote evolution; here we present neither a detailed reanalysis of his characters nor a precise alternative to his phylogeny of this group. Instead, we argue that Carroll's own procedure was formulated such that his negative conclusions about the assumptions of the phylogenetic method were inevitable. We contend that many of Carroll's objections to the phylogenetic method rest on faulty reasoning.

Carroll's most severe criticism of the phylogenetic method seems to be its ". . . assumption that the majority of derived features possessed in common by related groups are the result of inheritance from a common ancestor, rather than from convergence" (Carroll, 1982:104; but see Farris, 1983). For the early amniotes, Carroll (1982:102) finds that the distribution of derived features forms "an almost random mosaic" among his basic taxa. This leads him to conclude (Carroll, 1982:104) that "most of the derived character states recognized in two or more of the derived groups must be attributed to convergence." Thus, an important assumption of the phylogenetic method seems to be violated.

We certainly agree that rampant convergence can lead the systematist to incorrect phylogenetic conclusions. However, if Carroll's scenario about early amniote evolution is correct and his prior assumptions about basic taxa are accepted, then he has chosen to discuss *only* those characters that *must* be convergent (see Fig. 1). In Carroll's scenario (p. 106), the time span from the Early Pennsylvanian to the Early Permian saw the appearance of "a succession of derived groups that may all be traced to the protorothyrid stock." Therefore, any true synapomorphies evidencing a close relationship among two or more of these "derived"

groups must have arisen within Carroll's "Protorothyridae" (= Protorothyrididae). Carroll, however, is concerned with entirely different characters, specifically, those "in which the most primitive known members of each of the derived groups are *more advanced than the protorothyrids*" (Carroll, 1982:100, italics added). But if all the other groups of early amniotes are derived independently from "protorothyrids," then any such derived characters shared by two or more of these groups *must* by definition be convergent. Therefore, we do not find it suprising that Carroll (1982:102) finds no obvious congruence among these characters.

Critics of the phylogenetic method (Mayr, 1981; Carroll, 1982) argue that evolutionary parallelism and convergence pose particular problems for this method. Platnick (1977) demonstrates clearly that the opposite is true, namely that analysis of shared apomorphies provides an unambiguous method of identifying cases involving convergence. Such a determination is made by considering the distribution of the feature in question in relation to those of other derived features among the taxa concerned. For a given character distribution, parallelism/convergence can be shown to be either necessary or unnecessary to account for the distribution of particular derived characters among the terminal taxa (Platnick, 1977).

Convergence and parallelism refer to similarities derived independently rather than those inherited from a common ancestor. By definition then, an hypothesis of relationship must be established in order to support a claim of convergence. As Gaffney (1979) aptly states the case, "An argument for parallelism or convergence is simply an argument (often unstated) in favor of one phylogeny over an alternative one." Carroll (1982) provides no support for his alternative hypothesis of relationships. He presents no characters indicating that any particular "protorothyrid" shared a more recent common ancestor with one of his "derived" groups than with other "protorothyrids." Such evidence would be necessary to support his claim that 1) these "derived" groups were actually "derived from protorothyrids," and 2) that any particular derived characters shared by two or more of these "derived" groups (but not by "protorothyrids") are therefore convergent.

Given that Carroll's hypothesis about early amniote phylogeny is true, then all of the derived characters shared by two or more of his derivative (non-proto-

rothyrid) taxa are necessarily convergent. It is also possible, however, that Carroll's phylogeny is incorrect and that at least some of the derived characters shared by two or more of the other amniote taxa are true synapomorphies, characters shared because they were inherited from a common ancestor with a similar condition. Carroll dismisses this possibility, presumably because he doubts the significance of similar derived features shared by groups with different adaptive patterns in demonstrating a close common ancestry (see below). Such a superficial dismissal of characters seems to us to be ill-founded.

Possible relationships suggested by shared, derived features are often inappropriately discounted when the derived features in question are thought to be adaptive for a particular lifestyle. It is argued that such features are not phylogenetically meaningful because they are predisposed to convergence. We do not deny the *possibility* of convergence; however, it is not logical to conclude summarily that such shared, adaptive features *are* convergent and, therefore, that the suggested relationships do not exist. Because a phylogeny is required to demonstrate convergence in a particular character, the synapomorphic nature of such a shared, derived feature and the relationships suggested by it cannot be dismissed until other derived features are found to evidence different relationships, that is until an alternative phylogeny is proposed and supported.

Many of Carroll's arguments are strongly tied to the concept of adaptation, particularly to the concepts of the adaptive zone and of adaptive radiation (see also Van Valen, 1971, 1978). For example, Carroll (1982: 104–105, italics in original) states:

> "A distinction should be made in the relative significance of similar derived character states *within* groups that share a common adaptive and structural pattern, and *between* groups that have adapted to different ways of life.
>
> The presence of shared derived characters can be useful in recognizing members of *particular* groups. . . . On the other hand, similar derived characters present in groups with fundamentally different adaptive patterns may be of less significance in demonstrating a close common ancestry."

We find this approach undesirable because it is so dependent on subjective initial decisions of what constitutes an adaptively unified group. For example, the "pelycosaurs" are said to have contained both large and small carnivores and two major groups of herbivores (Carroll, 1982:93)—groups seemingly very different in adaptation. Had Carroll followed his own reasoning and recognized these adaptive types as his basic taxa, he would never have been able to conclude that together they formed a larger group, his "pelycosaurs." Carroll (1982:93) again contradicts himself by accepting an exclusive common ancestry among groups even more divergent in their adaptations: "pelycosaurs," "therapsids," and mammals. The the-
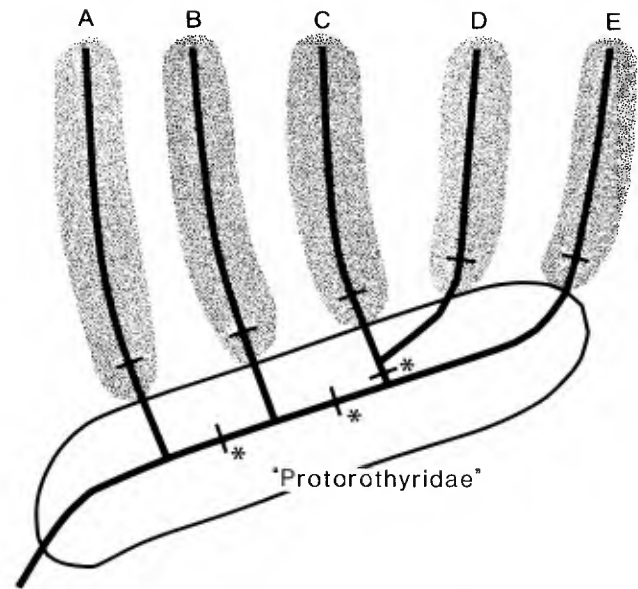


FIGURE 1. Phylogenetic diagram depicting derivation of various "derived" amniote groups (shaded bubbles A–E) from an "ancestral Protorothyridae" (unshaded bubble) as hypothesized by Carroll (1982). Only derived characters that arose within "Protorothyridae" (bars with asterisks) can provide evidence for a close relationship between two or more of the "derived" lineages. Nevertheless, Carroll (1982) discusses only derived characters not present in any protorothyrid (bars without asterisks). Given these relationships, any such characters shared by two or more of the groups A–E are necessarily convergent.

ory of evolution predicts that living things form a hierarchy of groups within groups. Because evolutionary descent is accompanied by the divergence of lineages, the more inclusive the group, the less likely that its members will be very similar in adaptation. This does not, however, preclude the possibility of recognizing more inclusive groups. Carroll certainly recognizes the group Amniota, despite the very different adaptive zones occupied by its component subgroups. We predict that groups less inclusive than Amniota, but containing two or more of Carroll's basic taxa, will eventually be recognized. Some progress is already being made along these lines (Gaffney and McKenna, 1979; Reisz, 1981).

Another perplexing aspect of the passage quoted above is Carroll's seeming implication that one can discover little more about relationships than the membership of groups already assumed to exist. Carroll's statement that shared, derived characters are useful for recognizing the members of particular groups is logical—provided that the groups are already characterized. Carroll's examples show that his "groups" are his basic taxa (pelycosaurs, captorhinids, etc.), whose interrelationships are the object of investigation. But Carroll doubts the significance of derived characters shared by members of these different "groups" in demonstrating a close common ancestry between them.

Thus, he faces the dilemma of being unable to demonstrate anything more than what he has initially assumed to be true, namely, the existence of his basic taxa as separate entities.

Carroll never explains why derived characters shared by groups that differ fundamentally in adaptive pattern might be insignificant in demonstrating a close common ancestry. Groups differing fundamentally in adaptation, such as the early amniote taxa discussed here, would be subject to dissimilar selective forces. Therefore, it seems unlikely that the derived characters shared by such groups were shaped convergently by adaptation to similar selective forces. A more reasonable explanation for two or more of the groups sharing these derived characters is inheritance from a common ancestor, i.e., a close relationship among the groups.

One major difference between the traditional approach advocated by Carroll (1982) and Hennig's (1966) phylogenetic method is recognition of paraphyletic groups in the traditional approach. Although justifications for the formal recognition of such taxa are often couched in biological terms, that is, in terms of theories about the evolutionary process (e.g., adaptation), paraphyletic groups only disguise a lack of knowledge. Perhaps there really are no characters that will serve to link the major groups of amniotes, and we cannot say how they are related to one another. This is a precise statement about our lack of knowledge. Some of these groups, however, must share a more recent common ancestor with one another than they do with any of the other groups (even if that common ancestor did not look very different from the most recent common ancestor of all of them). Therefore, when Carroll (p. 107) hypothesizes that each of these lineages "may have evolved separately from the conservative protorothyrid stock," he has not solved the problem. Instead, a lack of knowledge is obscured by the formal term Protorothyridae. For now, ironically, we "know" the evolutionary history of the amniotes (i.e., adaptive radiation) even though we have no idea how its subgroups are interrelated.

Paraphyletic higher taxa, such as "Protorothyridae," are often called on to serve as "ancestors" when potential ancestors are unknown. But if species are the most inclusive actively evolving entities (Wiley, 1979), then they are also the most inclusive entities that can be ancestors. Supraspecific taxa, which do not evolve except as a result of the evolution of their constituent species (Hull, 1980), cannot give rise to anything, i.e., they are not biologically meaningful ancestors (Wiley, 1979, 1981). Often no known species meets the specifications of an ancestor in all of its characters. In such cases paraphyletic higher taxa are very accommodating, for they can always be defined in such a way as to fit the character specifications of an ancestor (although they will not meet the requirement that an ancestor is a species). Unfortunately, such paraphyletic "ancestral" higher taxa convey a false impression of knowledge, as is revealed in the following passage from Charig (1982:431, italics in original):

"In any case, I cannot accept Patterson's contention that no useful information is conveyed by statements referring to paraphyletic groups. Presumably he would argue that the statement "Amniota originated from the Amphibia" is a meaningless statement, simply because the Amphibia are a paraphyletic taxon; nevertheless, he would agree that the Tetrapoda are a natural monophyletic group, a clade, within which are nested the Amniota as a subordinate clade. This means—if an evolutionary interpretation be permitted—that the Amniota originated within the Tetrapoda. But they could not have originated from themselves; they must have orginated from *other* tetrapods. And the only other tetrapods, by definition, are the Amphibia!"

Charig misses the point. Given that 1) Tetrapoda is monophyletic, 2) Amniota is monophyletic, and 3) Amniota is a subset of (i.e., originated within) Tetrapoda, no additional phylogenetic information is conveyed by 4) naming a group ("Amphibia") for non-amniote tetrapods and declaring that amniotes originated from them. This would simply be saying that amniotes originated from tetrapods that were not amniotes. The statement "Amniota originated from the Amphibia" is not meaningless, but given that amniotes are a subset of tetrapods it is certainly redundant.

Carroll offers an argument purporting to demonstrate that "Protorothyridae" (formerly the Romeriidae, now excluding *Romeria*) is a natural group. This argument, however, suffers from his failure to distinguish between the meanings of two different pairs of terms, primitive and derived versus generalized and specialized. The former pair refers to the relative time of origination of characters in a transformation series, the latter is an ecological concept referring to the breadth of resources used. Carroll seems to equate specialized with derived, as can be seen in the following passage (Carroll, 1982:91, italics in original):

"Although protorothyrids exhibit the primitive character state for nearly all the skeletal features recognized among early reptiles, this should *not* be considered as defining the group on the basis of primitive characters.

Judged on the basis of Paleozoic amphibians, especially the advanced anthracosaurs, the protorothyrids are highly specialized in their small body size, relatively small mobile skull, and light limbs. Of equal importance are their probable habitat and dietary specializations, resembling those of primitive modern lizards. This adaptive pattern characterizes the protorothyrids after a period of some 35 million years. This is as specialized a way of life, relatively [sic] to that of other early tetrapods, as the carnivorous way of life of early pelycosaurs, or the durophageous specializations of captorhinids."

Carroll's argument fails when one realizes that it is possible for a character to be both primitive and specialized. It does not matter that "protorothyrids" are

specialized as small insectivores. If the other amniote groups were derived from "protorothyrids" as Carroll claims (but does not support), then the characters of "protorothyrids" as a whole can only be primitive relative to those of other amniotes.

Another problem with the passage quoted above is Carroll's apparent failure to accept the consequences of the relative nature of the terms primitive and derived. "Protorothyrids" may be derived in certain features relative to Paleozoic "amphibians," but so are all amniotes. Carroll (1982:91) admits that "protorothyrids" ". . . share few if any advanced character states, relative to other early amniotes." Therefore, given that "protorothyrids" are amniotes, they can only be distinguished from other amniotes by their primitive (unmodified) characters. We do not understand how Carroll can claim otherwise.

Perhaps what Carroll really considers to be natural about paraphyletic groups is that the members of such groups supposedly share common adaptive morphotypes (see also Van Valen, 1971, 1978). But the morphologies seen in the living world do not fall on a single line of increasing adaptation. Part of modern evolutionary theory is the concept of mosaic evolution (Mayr, 1969), in which different characters undergo change in different groups and the same characters change at different rates in different groups. The practice of recognizing paraphyletic grades as formal taxa is compatible with notions of evolutionary progress from "lower" to "higher" forms or with the pre-evolutionary *scala naturae*; it is incompatible with modern evolutionary theory.

A curious feature of traditional evolutionary systematics is its failure to discriminate consistently between two very different kinds of groups, paraphyletic groups and strictly monophyletic groups. The traditional evolutionary systematist considers both of these to be monophyletic in a broader sense (Ashlock, 1979; Mayr, 1974) and, therefore, to be both natural and equally valid as formal taxa in phylogenetic classifications. There are, however, important differences between paraphyletic and strictly monophyletic groups, differences that call into question the status of paraphyletic groups as anything but artificial constructs.

The ambiguity of traditional evolutionary classifications is seen upon examination of a few of the taxa that this system has produced. Here we find in seemingly equivalent (monophyletic, in the broad sense) taxa an unexpected difference in violability. Given sufficient evolutionary change, it is permissible to remove lineages from certain (paraphyletic) taxa. For example, Aves and Mammalia are said to have evolved from the paraphyletic "Reptilia" as has Amniota from the paraphyletic "Amphibia." But lineages never evolve out of other (monophyletic) taxa. Even though caecilians and most snakes lack legs, they are and will always be tetrapods. Since traditional evolutionary systematists grant both paraphyletic and strictly monophyletic taxa equivalent status, they seem not to appreciate this fundamental difference.
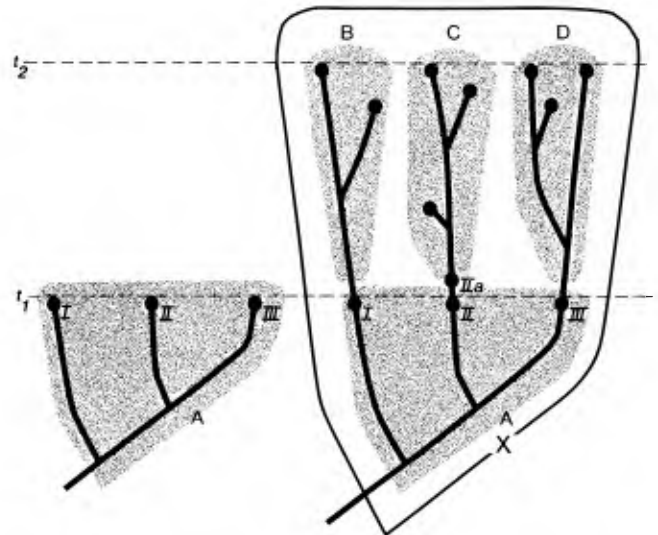


FIGURE 2. Time, monophyly, and paraphyly. See text for explanation.

The failure of traditional evolutionary systematists to appreciate the difference between paraphyletic and monophyletic groups allows them to offer a curious argument in favor of the natural status of paraphyletic taxa. Carroll (1982:87) writes: "Early amniotes may be viewed today as a phylogenetically heterogeneous assemblage (or paraphyletic group), for they include the ultimate ancestors of mammals and birds, as well as of the modern squamates, crocodiles and turtles. Yet, within the context of the Paleozoic, they were a monophyletic group, with a close common ancestry." The argument usually continues: if these organisms formed a natural, monophyletic group in the Paleozoic, then they can still be viewed as a natural group today. Surely the mere passage of time cannot change the natural status of a group.

In order to evaluate this argument, let us first assume that the phylogeny of the organisms involved is known (Fig. 2). At time $t_1$, taxon A, perhaps the "Protorothyridae," is indeed a natural, monophyletic group. At $t_2$, taxon A is paraphyletic and, in the opinion of many systematists, no longer natural. How has time changed the status of the group? It hasn't. At $t_1$, "Protorothyridae" is synonymous with Amniota, and both are natural (monophyletic) groups. At $t_2$, Amniota (taxa in bubble X on the right side of the figure) is still a natural (monophyletic) group. "Protorothyridae" and Amniota, however, are no longer synonymous. Instead, the direct descendants of the former have been placed in different groups. Even though some "protorothyrids" (e.g., II) are more closely related to some nonprotorothyrids (IIa) than they are to other "protorothyrids" (I or III), these nonprotorothyrids are placed in different groups (B, C, D). It is not the mere passage of time that has changed the status of the group, but the systematist's (not nature's) decision to remove certain direct descendants from the group.

There is another problem with paraphyletic grade taxa, namely that by creating such taxa the systematist invites misuse of classifications by biologists untrained in systematics (although even trained systematists are guilty of these errors). These biologists can now talk about such things as variation, geographic and temporal distribution, and extinction of taxa whose fates have been determined as much by human predilections as by biological processes. Can we honestly say that after 35 million years the "Protorothyridae" became extinct even though some of them may have been the direct ancestors of the vast array of living amniotes? What does it mean to label this group "conservative" (Carroll, 1982:103) if some of its members eventually gave rise to organisms as different as bats, whales, turtles, snakes, and birds?

Throughout this paper we have referred to Hennig's (1966) method as the phylogenetic method, as he originally called it. Although this method is currently more widely known as cladism or cladistics, we have deliberately avoided these terms. Too often cladism is considered to represent an *alternative* to traditional phylogenetic methods (e.g., Carroll, 1982). Although this may be true of some of cladism's more recent subdisciplines (Nelson and Platnick, 1981; Patterson, 1982), the phylogenetic method that Hennig formulated is not. Instead, Hennig's method is an elaboration of the kinds of evidence than can logically be used to make phylogenetic statements. As such Hennig's precepts are not an alternative to traditional phylogenetic methods, but a refinement of them. Although many of his critics do not appreciate this fact, Hennig's method remains a necessary part of any phylogenetic systematic study.

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