

# CLADISTICS AND THE FOSSIL RECORD: The Uses of History

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## INTRODUCTION

Cladistics, or phylogenetic systematics, was developed by the German entomologist Willi Hennig in the 1940s and 1950s and culminated in his book *Grundzüge einer Theorie der Systematik* (1950) and a later manuscript translated by D. Dwight Davis and Rainer Zangerl in 1966 as *Phylogenetic Systematics*. Though at first uninfluential outside a group of largely European entomologists, its rediscovery and promulgation in the 1970s by American ichthyologist Gareth Nelson and his colleagues eventually swept the major centers of biological taxonomy and systematics in North America and Europe [Hull (1988) reviews the history and sociology of this movement]. Its initial success was in the fields of fossil and recent fishes, notably in museums in New York, London, and Paris; but it soon spread to the other vertebrates, the invertebrates, plants, and unicellular forms, and has now become the dominant paradigm for systematic methodology.

The basic premises of cladistics are that only strictly monophyletic groups (i.e. those comprising *all* the descendants of a common ancestor) should be recognized and used, and that these groups (called *clades*) must be diagnosed by new evolutionary features (synapomorphies) that evolved in the common ancestor and were passed to its descendants. The nested patterns in which these synapomorphies are shared by different taxa are used to group them in an order of evolutionary descent and relationship. Classification becomes an objective exercise determined by the order of branching.

This apparently simple procedure has profound implications for the

studies of phylogeny (evolutionary relationships), taxonomy (the basis on which organisms are recognized and sorted), and classification (the ranking of taxa, traditionally in hierarchical but not necessarily parallel Linnean groups). For evolutionary biologists, cladistics also forces a specific phylogenetic structure upon typical questions posed about the evolution of function, physiology, adaptation, and behavior, as well as ecology (Brooks & McLennan 1990, Harvey & Pagel 1991). For paleontologists and geologists, a complementary set of questions and implications has arisen, and these form the focus of our review.

We begin with a brief summary of the principles and methods of cladistics, and discuss how these differ from traditional ones. We then show some implications of new cladistic analyses for paleontology and geology. First, phylogenetic relationships of many fossil groups have been elucidated or altered, and accordingly classifications have changed. For example, it is no longer possible (and it never was accurate) to speak of “fishes giving rise to amphibians, which gave rise to reptiles, which gave rise to mammals and birds.” Second, we provide some examples of paleobiological questions for which cladistics has provided new insights, a different perspective, or a more powerful test or explanatory framework. These include questions about diversity through time, rates of taxonomic change and turnover, problems of origination and extinction of groups, calibration of molecular evolutionary trees, the evolution of adaptations, and trends in ecological and biogeographic change. Third, and most importantly, we develop some ideas for questions and fields in which cladistics can alter traditional paradigms and provide new ways of thinking about old problems in paleobiology and macroevolution.

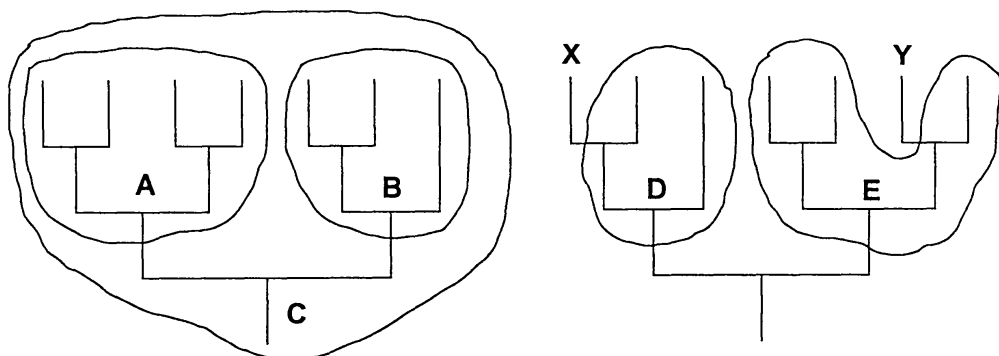
## PRINCIPLES AND METHODS OF CLADISTICS

Several texts and standard references (Eldredge & Cracraft 1980, Wiley 1981, Wiley et al 1991) explain in detail the basics of cladistics, and more advanced methods, computer programs, and philosophical questions are discussed in leading journals such as *Cladistics*, *Systematic Biology* (formerly *Systematic Zoology*), *Systematic Botany*, and the *Annual Review of Ecology and Systematics*. Here we give only the barest of outlines using the simplest vocabulary possible.

A basic principle of evolution is that organisms are descended from their parents with heritable modifications that are then further passed on and altered in future generations. This implies that a particular modification seen in a given organism and its descendants, but not in its ancestors and relatives, is a character that has been introduced into the evolutionary pattern at a given point. Such characters, shared by organisms that derived

them from a common ancestor, are called *synapomorphies* (shared derived characters). The common possession of synapomorphies is the criterion used to unite taxa into *monophyletic* groups—the Holy Grail of cladistics. To be monophyletic, a group must include an ancestor and *all* its descendants. If it includes only some descendants, it is not monophyletic, but paraphyletic (Figure 1). For example, the earliest known bird, *Archaeopteryx*, shares dozens of synapomorphies with small carnivorous dinosaurs (Ostrom 1976; Padian 1982; Gauthier 1984, 1986). Because birds evolved from dinosaurs, which are reptiles, birds are cladistically considered members of the Reptilia, and “reptiles” are not monophyletic unless they include birds. Because monophyletic groups contain all the descendants of an ancestor, they cannot be said to “give rise” to any descendant groups. When monophyletic groups are found to be linked by synapomorphies, they are called *sister groups*. Among living reptiles, birds are the sister group of crocodiles, united with them in the Archosauria (Gauthier 1984, 1986).

In cladistics, taxa are *diagnosed* by synapomorphies, and *defined* by ancestry (Rowe 1987). Because any two organisms must share a common ancestor at some point, however remote in evolutionary history, they and all descendants of that common ancestor are defined cladistically to form a monophyletic taxon. We use synapomorphies to diagnose monophyletic groups, which we hypothesize share these features because they have inherited them from a common ancestor. It follows that all characters must be synapomorphies at some taxonomic level. Feathers are unique to birds, and so help to diagnose them as a group; but the possession of feathers cannot tell us the difference between a scrub jay and a Steller’s



*Figure 1* In the diagram at left, groups A, B, and C are monophyletic, because they include *all* the descendants of a common ancestor. In the diagram at right, groups D and E are paraphyletic (not monophyletic), because they exclude some descendants (X and Y) of their common ancestor.

blue jay: The character is too general. However, specific *features* of the feathers (character states) may indeed differentiate the two species. Hence every character is derived at some level, but general (original or “primitive”) at another.

A cladistic analysis of a group of taxa is generally begun by selecting characters with varying states that can be analyzed to determine which state is ancestral or original for the group and which is (or are) derived. This is called *polarization* of characters, and it is usually done with reference to the characters of one or more outgroups (Maddison et al 1984). These data are arranged in a matrix in which the rows and columns represent taxa and characters. Cells are coded with numbers or symbols representing the character states of each character for each taxon. The codes can be used to signify general and derived states. Computer programs such as HENNIG86 (Farris 1988), PAUP (Swofford 1991), PHYLIP (Felsenstein 1991), and MacCLADE (Maddison & Maddison 1992) group taxa successively according to the distribution of the synapomorphies that they share, and link succeeding remote groups to these until all are linked. Many programs help to deal with conflicting and unknown character information—subjects that are beyond our scope here [but see Wiley et al (1991) for further details and an introduction to the primary literature].

According to its proponents, the principal advantage of the cladistic system over others is that it is unrelentingly evolutionary; that is, it is fundamentally concerned with the branching order of evolution. Its insistence on monophyletic groups means that many familiar and long-hallowed taxa must be completely reorganized or eliminated entirely. To its detractors, cladistics unnecessarily eliminates traditionally useful and often ecologically or morphologically cohesive groups in the name of monophyly, but the benefits are not worth the losses. Rather than discuss that question here, we choose to show some examples of how cladistic methods have changed our understanding of the evolution of life and of important events in its history. We do not pretend that cladistics is a panacea for all paleontological questions, but we think that the test is as much in the pragmatics as in the ideology.

## SOME NEW CLADISTIC PHYLOGENIES AND THEIR IMPLICATIONS

We noted above that one major implication of cladistics is that its insistence on monophyly tends to invalidate many long-familiar groups, or restructure them radically. Some major examples follow. These are based on de Queiroz & Gauthier's (1990, 1992) terminology from their phylogenetic taxonomy of craniates.

### *Cambrian Arthropods*

Significant evolutionary changes in the fossil record traditionally have been reflected by expansions of taxonomic rank. The appearance of new phyla or other higher taxa in the fossil record indisputably focuses attention on events in the history of life. Sudden radiations such as the “Cambrian explosion,” or the presence of taxa that are not readily included in living groups (e.g. the Ediacaran and some components of the Burgess Shale), are typically the subject of tremendous speculation and scenarios. These fossil problematica are often assessed in terms of either their morphological or taxonomic differences from living taxa, but important phylogenetic questions are seldom based on an explicit framework of relationships.

A recent exception to this has been the work of Briggs & Fortey (1989) and Briggs et al (1992), who have addressed the question of Cambrian arthropod phylogeny and whether or not disparity was greater in the Cambrian than now (see Gould 1991, Foote & Gould 1992). Although Gould (1989) clearly distinguished between taxonomic diversity and morphological disparity, his conclusion that morphological disparity was greater in the Burgess Shale arthropods than in living groups was not tested phylogenetically (see also Gould 1991). Subsequent phylogenetic analyses by Briggs & Fortey (1989) and Briggs et al (1992) failed to support greater disparity. Their analyses suggested that extinct Cambrian taxa dominate one arthropod subclade while the remaining taxa are scattered among living groups (Figure 2). Traditional overemphasis of unique character combinations (*autapomorphies*), combined with the use of paraphyletic grades such as the “Trilobitomorpha,” have obscured detailed relationships and quantifications of disparity.

### *Monoplacophorans*

Monoplacophorans are another Cambrian group whose evolutionary history needs to be reinterpreted by cladistic analysis. These cap-shaped Early Paleozoic molluscs were well-studied by Knight (1952), and his reconstructions have proven remarkably accurate. Formerly known only from Cambrian-Silurian deposits, monoplacophorans were recovered alive and well in the deep sea in 1952. Because of the antiquity of the group and its unique molluscan morphology, it was immediately christened “a living fossil” and incorporated into molluscan phylogeny as the putative ancestor of the living molluscan classes. However, without a rigorous cladistic analysis it has not been possible to sort out primitive from derived characters; nor has there been sufficient consideration of which autapomorphies might be misinterpreted as ancestral characters.

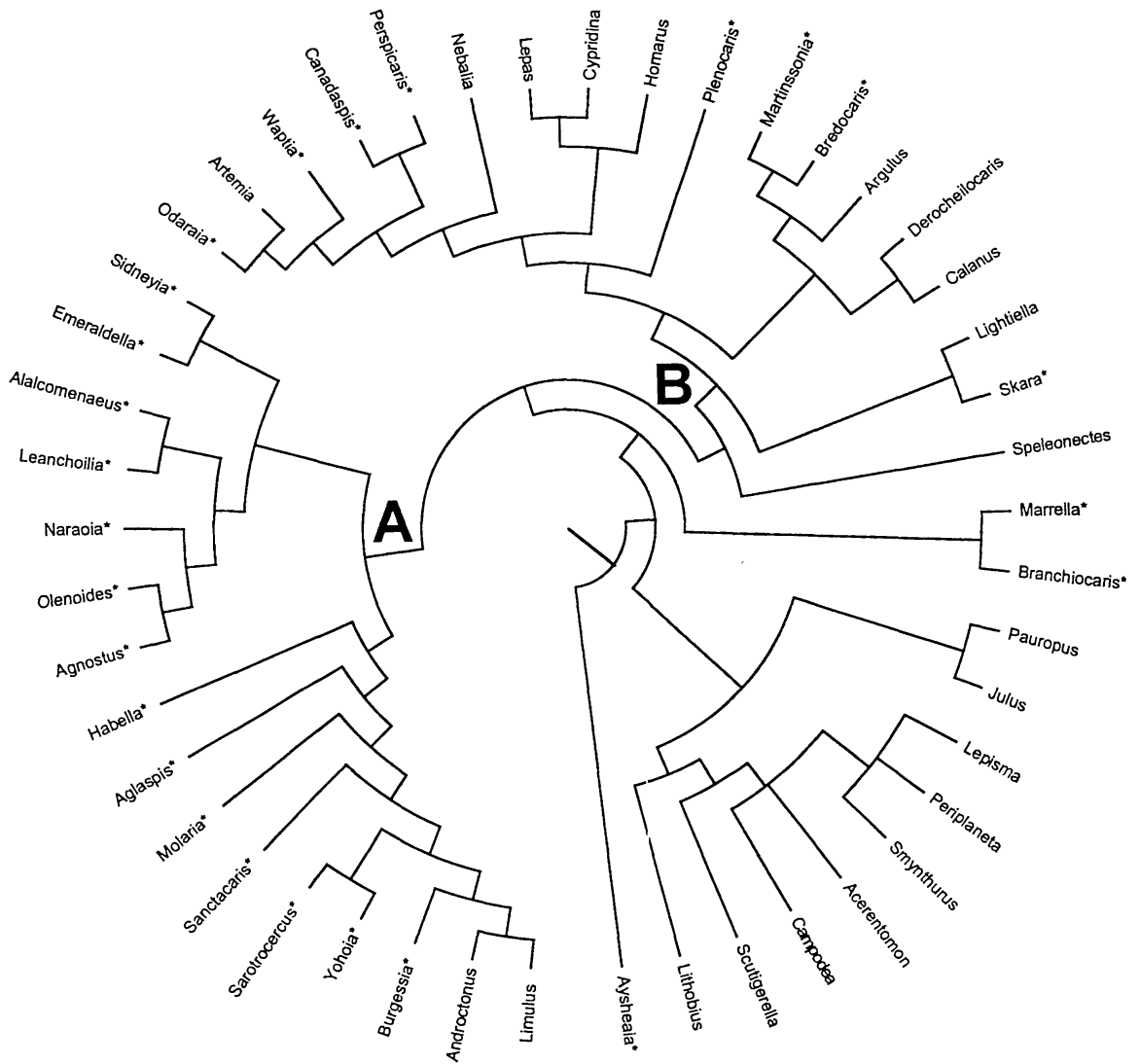


Figure 2 Cladogram of Cambrian and living arthropods. Cambrian arthropods are marked with an asterisk. In subclade A 87.5% of the taxa are extinct Cambrian taxa; in subclade B only 44.4% of the taxa are extinct. Differential extinction rates in different subclades exacerbate patterns of disparity. After Briggs et al (1992).

Although paleontologists, geologists and zoologists do not dispute that monoplacophoran habitats have changed considerably through geologic time, there has been little discussion of the potential for correlated anatomical changes. Cladistic analysis provides a framework against which to evaluate character distributions and transformations in the Monoplacophora. These analyses (Stuber & Lindberg 1989) advise that components of the radulae, shell structure, nervous system, excretory system, buccal mass, and other features all display the autapomorphic condition:

Their character states are unique to the monoplacophorans and not primitive for the Mollusca. It appears that monoplacophorans did not experience descent without modification for the last 350 million years as previously thought. Based on a cladistic analysis they are highly modified animals with numerous autapomorphies, and possible character reversals. Thus, the use of monoplacophorans as “primitive” taxa to polarize characters in the other molluscan classes is a dangerous practice.

### *Fishes*

It has long been held that tetrapods evolved from some aquatic form that would normally be called a “fish.” Hence in the phylogenetic system of cladistics, “fishes” must be paraphyletic, unless all vertebrates are called “fishes.” But we already have a word for this: vertebrates. The closest living forms to tetrapods are the lungfishes, and they and the tetrapods together form a clade called Choanates (because they all have internal choanae, or nostrils that open inward). The coelacanth joins the choanates as the Sarcopterygia (“fleshy-fins”). These join the rayfinned fish, which includes nearly all the forms usually considered “fishes,” in a group called Osteichthyes (bony fish). The sharks and their allies (Chondrichthyes, or cartilage fish) join the Osteichthyes in a group called Gnathostomi (jawed mouths), and they are thereby separated from other vertebrates that lack jaws, the lampreys. All these groups together form a clade called Vertebrata, because they have vertebrae; the hagfishes do not, but they do have at least a rudimentary cranium, so they and the vertebrates together form the Craniata.

Figure 3 demonstrates this branching sequence, together with the new names of groups in the phylogenetic system and some of the synapomorphies that diagnose them. We suggest that the name “Pisces” (colloquially, “fishes”), if it be used at all, be restricted to Actinopterygii (the living rayfins) and all the extinct bony fishes (Osteichthyes) closer to them than to Sarcopterygii. This would simplify and clarify the use of the term “fishes” in both technical and common senses, inasmuch as the vast majority of non-tetrapod craniate species (“fishes”) are actinopterygians, and their biology differs in fundamental ways from those of the other non-tetrapods. It can be seen readily that, whether or not this usage is adopted, “fishes” cannot have given rise to tetrapods. Rather, tetrapods evolved from within a group of choanate sarcopterygians—fleshy-finned forms with internal choanae, neither of which features are shared by rayfins. This is less confusing because it obviates trying to figure out how a trout or perch could have given rise to a tetrapod, what sorts of features it would have had to lose or gain, how the ecological transition was made, and so on. Instead, the rayfins are seen for what they are, a sidebranch of vertebrate evolution quite distinct from the sidebranch including tetrapods.

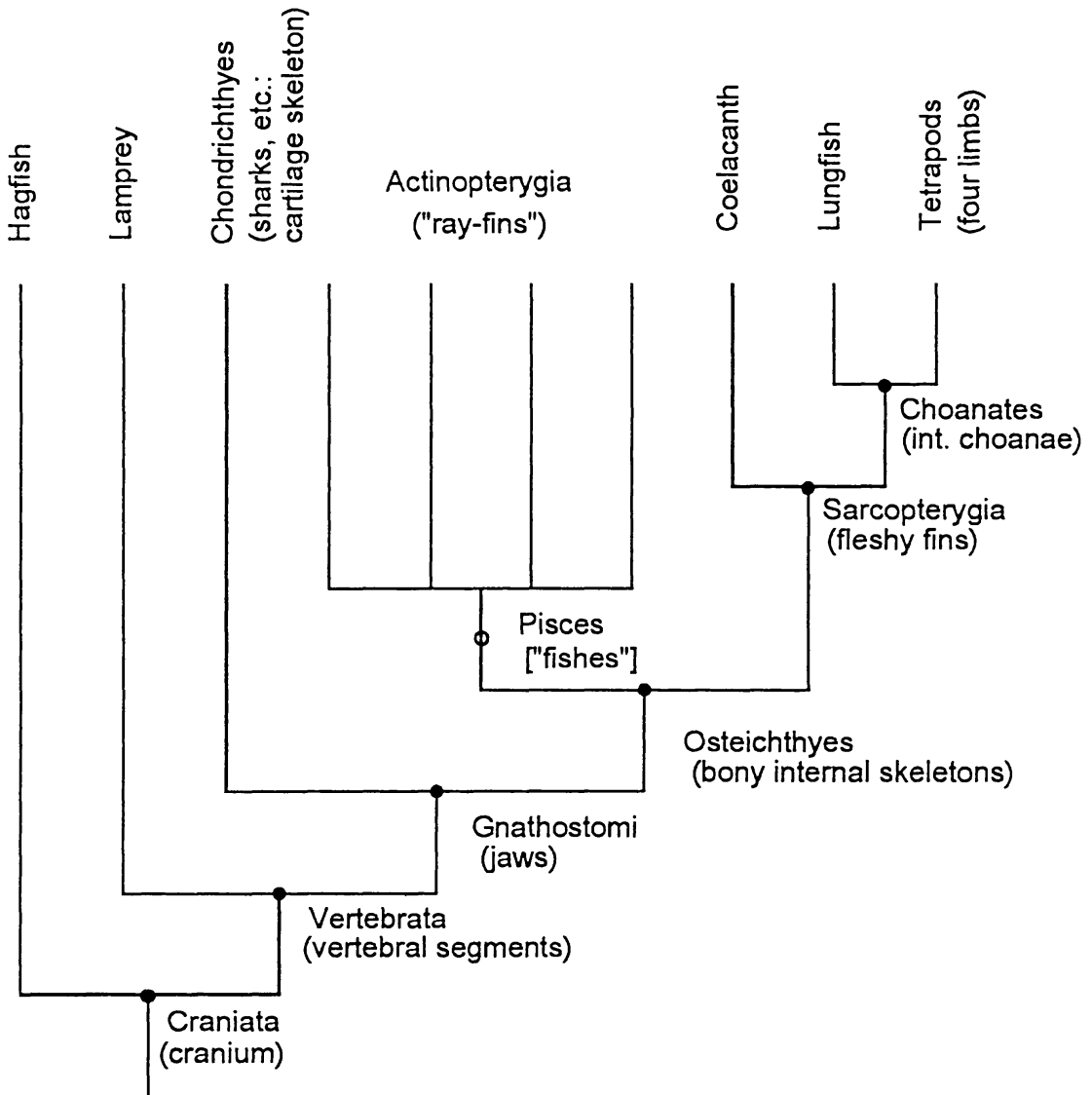


Figure 3 Tree of the basal vertebrate groups, including some major features of their evolution (synapomorphies, in parentheses), based on cladistic analyses. After de Queiroz & Gauthier (1992) and other references.

### *Tetrapods*

Similarly, the tetrapods have been restructured and renamed according to cladistic analysis (Gaffney 1980; de Queiroz & Gauthier 1992; Benton 1988; Novacek & Wyss 1986; Estes & Pregill 1988; Prothero & Schoch 1989; Gauthier 1984, 1986; Gauthier et al 1988a,b, 1989). A recent summary (after de Queiroz & Gauthier 1992) is diagrammed in Figure 4.



Amphibians are rightly seen as a sidebranch of tetrapod evolution, not as an amorphous basal mass of tetrapods out of which reptiles evolved. Amphibians are restricted to the living groups and all extinct forms closer to them than to living reptiles. Amphibians, in this sense, share features such as a broad flat skull, a double occipital condyle, the loss of a finger, and vertebrae in which the intercentra dominate the pleurocentra. All these features would have to be lost or reversed for amphibians to be the “ancestors” of reptiles, as traditionally taught.

In fact paleontologists have recognized for some years now (Panchen 1980, Heaton 1980, Milner 1988, Panchen & Smithson 1988, Gauthier et al 1989) that a collection of Carboniferous tetrapods called “anthracosaurs” (from their discovery in coal deposits) are less closely related to proper amphibians than they are to *Seymouria*, *Diadectes*, and other forms traditionally considered “reptiles” or near-reptiles. Placing them all in a clade

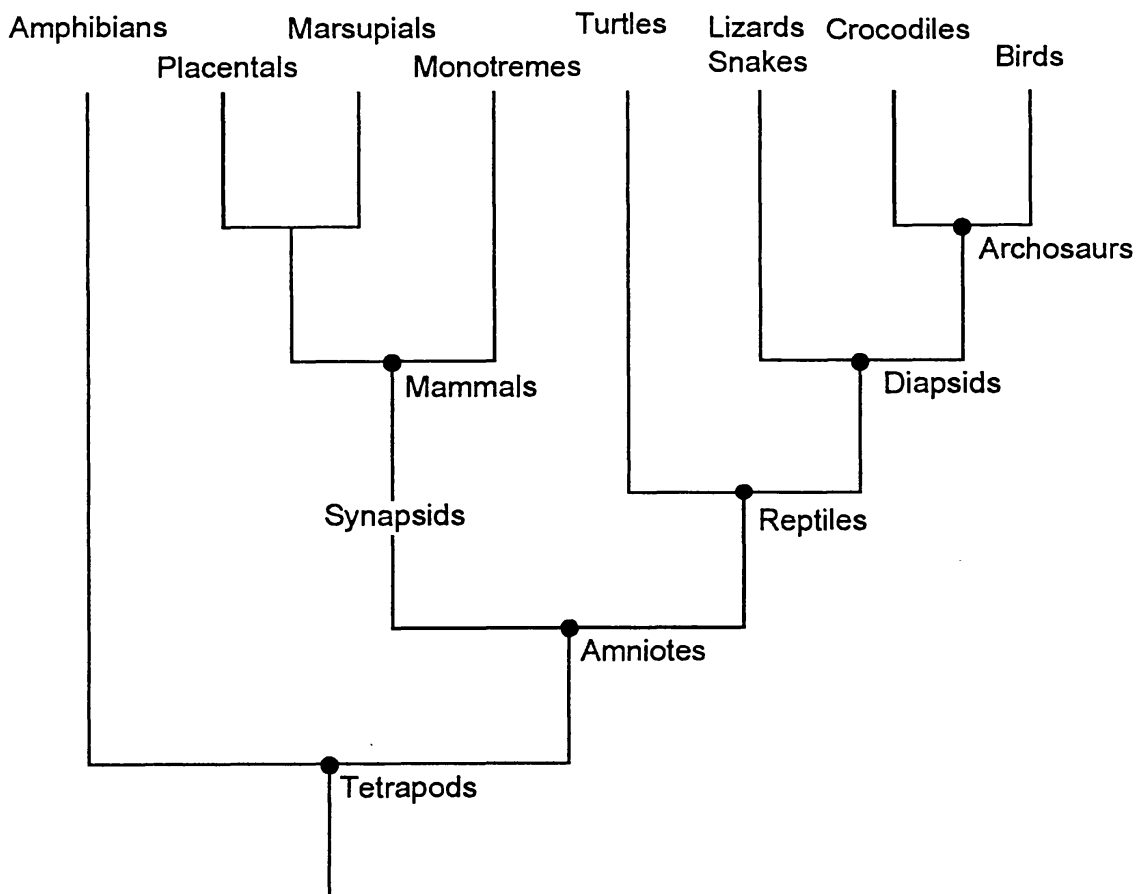


Figure 4 Tree of the major groups of living tetrapods, based on cladistic analyses. After de Queiroz & Gauthier (1992) and other references.

called Anthracosauria emphasizes this shared ancestry. However, we no longer consider that this group gave rise to “reptiles.” Reptiles are one branch of a more inclusive clade called Amniota, named for the amniote egg that improves nourishment, resists desiccation, and frees the life cycle from an aquatic or humid stage necessary to keep the egg from drying out. Amniotes evolved from anthracosaurs that were largely terrestrial, with improved limbs and vertebrae for locomotion and a lengthened, more mobile neck for feeding.

The first amniotes diversified quickly during the later Carboniferous into several groups that appeared almost simultaneously in the fossil record (Carroll 1988, Gauthier et al 1988b). One group is distinguished from the others by a single opening in the temporal region (the side of the skull behind the eye); animals to this point had no such openings. This “one-holed” group is called the Synapsida, and its members include the familiar fin-backed *Dimetrodon*, the two-tusked dicynodonts, and the mammals. Another group evolved enlarged suborbital openings in the bottom of the skull, and a suite of other features; these are the Reptilia proper, which include turtles, lizards, crocodiles, and so on. Within this group a substantial Permo-Carboniferous diversification (Carroll 1988) was succeeded by differential extinctions from which two major groups now survive. One group retained the no-holed temporal region, lost teeth, and evolved a shell; these are the turtles (Chelonia). Another group evolved not just one, but two temporal openings; these are called diapsids, and they contain the remaining reptiles. Their relationships were cladistically sorted by Gauthier and co-workers (Gauthier 1984, 1986; Gauthier & Padian 1985; Gauthier et al 1988a,b,c) and substantial progress continues in this group (Sereno 1986, 1991; Benton & Clark 1988; Evans 1988; Rieppel 1988; Cracraft 1988; Frost & Etheridge 1989; de Queiroz 1987). Perhaps of greatest interest is that the conclusion that birds evolved from small theropod (carnivorous) dinosaurs in the mid- or Late Jurassic has been firmly cemented by over 200 synapomorphies, thanks to subsequent cladistic analyses (Gauthier 1984, 1986; Gauthier & Padian 1985; Cracraft 1988; Sereno & Rao 1992; Perle et al 1993). This phylogenetic grounding provides a strong basis for approaching more process-oriented questions, such as how feathers and flight evolved, as we discuss below.

With new cladistic analyses such as these, the long-familiar and perpetually confusing term “mammal-like reptile” has now gone by the boards. This misnomer arose from the conception that the earliest amniotes were reptiles. As cladistic analysis shows, living reptile groups and their extinct relatives did not appear until well after their split with the group leading to mammals. Hence the ancestors of mammals never were reptiles, but were amniotes, like the ancestors of reptiles. To call these

forms “mammal-like reptiles” is as nonsensical as calling the ancestors of turtles and diapsids “reptile-like mammals.” One implication of this revision is that no living reptile can be considered a model for “primitive” amniote structure, function, physiology, or ecology. By studying characteristics commonly shared by living reptiles and mammals, and tracing the evolution of these characters in the extinct relatives of both branches, we can arrive at a more reasonable picture of what the first amniotes were like (Heaton 1980, Gauthier et al 1988a,b).

Mammals themselves have been subjected to extensive phylogenetic analysis using morphological evidence from living and fossil forms, as well as molecular evidence (Novacek 1992; papers in Benton 1988), though the congruence between morphology and molecules is not always ideal (Patterson 1987, McKenna 1987, Novacek 1992). Among fossil mammals, much work has been done within the major orders of mammals (e.g. Prothero & Schoch 1989, Benton 1988), as well as with determining the relationships of mammalian orders to each other. Much of this work is inconclusive because phylogenetic analyses fail to produce a clear branching pattern: Some taxa are too transformed to relate easily to a nearest known neighbor; there is rampant convergence in dental, cranial, or post-cranial features; crucial fossil taxa are missing parts or missing entirely; molecules have been found to be as plastic and potentially misleading as anatomy when it comes to indicating phylogenetic pathways. Nonetheless, some clear signals are emerging. Some mammalian groups, such as Condylarthra and Insectivora, have been broken up or greatly restricted in membership, because some of their members have been found to be closer to other groups, or because they were held together as a group only by primitive characters, not shared derived ones. Insectivora is generally abandoned in favor of the use of the several component taxa, such as Lipotyphla and Menotyphla, that can be constituted as monophyletic groups (Novacek & Wyss 1986, Novacek 1992). The fossil Creodonta, long thought to contain the ancestors of Carnivora, now turn out to be an entirely different group with no ancestral role (P. D. Polly, in preparation). Both Carnivora and Ungulata (hoofed mammals) were traditionally thought to have evolved from early Tertiary Condylarthra, but this latter group as traditionally constituted contains many forms lumped together only by primitive features. The hoofed mammals and some other taxa (sirenians, tubulidentate anteaters, and whales) appear to form a natural group, and the most primitive known fossil whales have limbs with a mesaxonic (even-toed) pattern seen in artiodactyl ungulates, as well as some early Tertiary forms usually included in the Condylarthra. Carnivorans and creodonts, traditionally grouped together, now appear more closely related to different mammalian radiations.

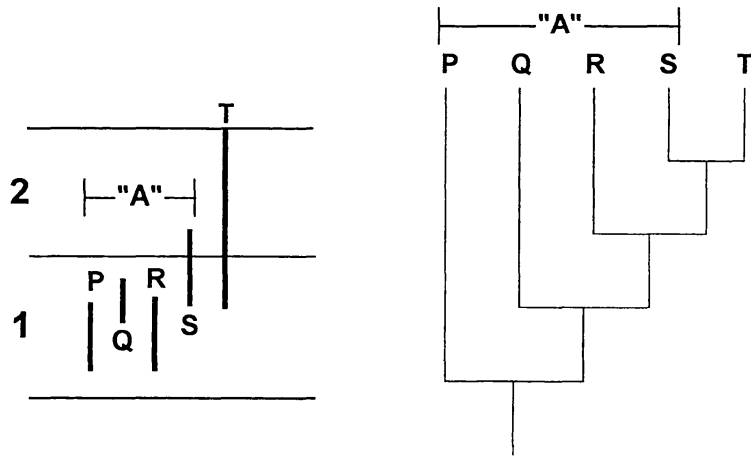
## IMPLICATIONS OF CLADISTICS FOR PALEONTOLOGY AND PALEOBIOLOGY

### *Cladistics and Stratigraphy*

As any geologist can readily appreciate, fine-scaled biostratigraphy depends on fine-scaled taxonomic identifications. Where fossils are abundant, and the record of index fossils is good, as in the records of most planktonic marine organisms used in correlation, identifications can normally be made to the species level. However, for deposits in which the fossil record is poorer, the specimens rarer, and the representation largely incomplete, as in many or most terrestrial environments (Padian & Clemens 1985), correlation at the species level may not be possible. It is therefore all the more important that biostratigraphic correlations that are forced to use supraspecific taxonomic levels be restricted to closely analyzed monophyletic groups (Padian 1989a). Paraphyletic groups may suggest both unnaturally short and long ranges, which can suggest spurious correlations. Revising paraphyletic groups and forming monophyletic groups from them frequently changes substantially our picture of taxonomic diversity across major boundaries, for example those associated with mass extinctions (Padian & Clemens 1985; Benton 1988, 1989a,b).

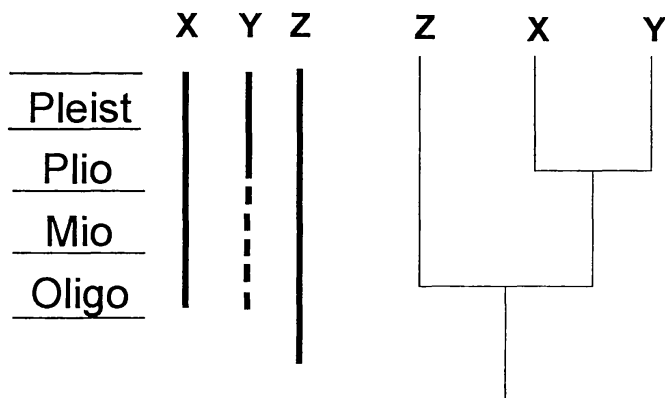
For example, consider a paraphyletic group "A" (Figure 5), which comprises the taxa P, Q, R, and S, but not T. The stratigraphic ranges of the individual taxa in "A" are not congruent: P, Q, and R span various ranges in time period 1, while S and T are found in both periods 1 and 2. In traditional usage, the range of taxon "A" (P+Q+R+S) is hardly distinguishable from that of T, because both "groups" are found in both time periods. But now consider the cladogram in Figure 5. S is the sister taxon of T, which suggests that S has been traditionally included in "A" on the basis of primitive features, not synapomorphies (shared derived features). In fact, no features characterize group "A" that are not shared by T. "A" therefore has an artificially extended range. Using stratigraphy, we see that no members of "A" except S survive into time period 2. Cladistics tells us that this is logical, because S and T are sister groups. If S is included in the paraphyletic group "A," it is less useful for stratigraphic purposes. The survival of S into time period 2 does not imply anything more; but if S is considered a member of the spurious group "A," the stratigraphic picture is muddled.

Other direct inferences about stratigraphic and temporal ranges can be made on the basis of cladistic analysis. For example, if X and Y are sister groups, and a member of group X is found in the Oligocene, then group Y must also have been present by the Oligocene, even if we have no fossils of its members (Figure 6). Norell (1992) has discussed these "ghost



*Figure 5* How paraphyletic groups confound biostratigraphic refinement. (*Left*) The stratigraphic ranges of the individual taxa in A are not congruent: P, Q, and R span various ranges in time period 1, while S and T are found in both periods 1 and 2. Thus, the range of taxon "A" (P+Q+R+S) is hardly distinguishable from that of T, because both "groups" are found in both time periods. (*Right*) However, when a cladistic approach is taken, S is the sister taxon of T, which suggests that T has been traditionally included in "A" on the basis of primitive features, not synapomorphies (shared derived features). In fact, no features characterize group "A" that are not shared by T. "A" therefore has an artificially extended range.

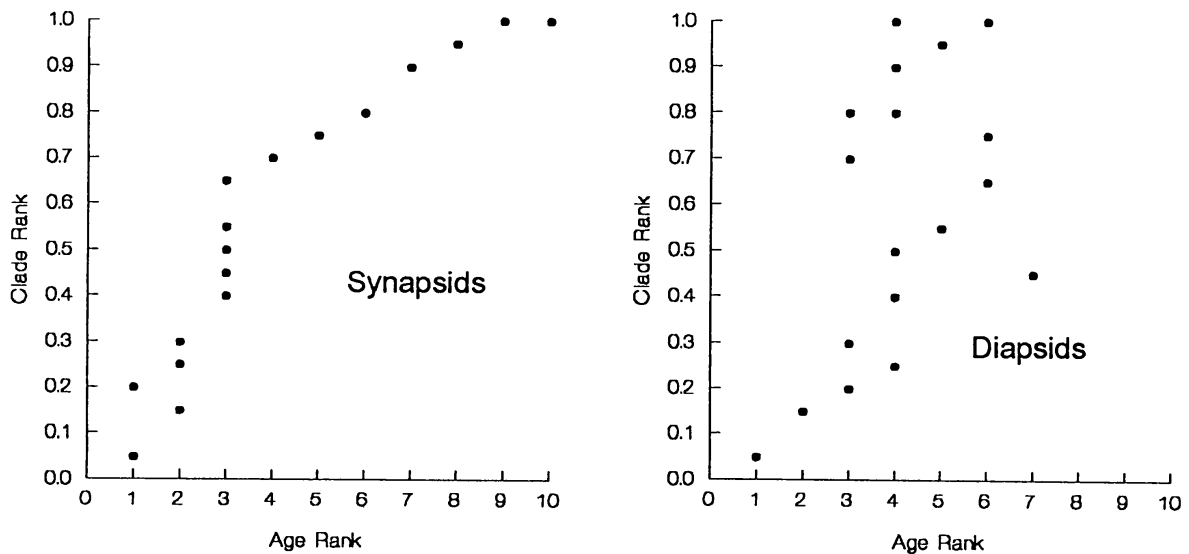
lineages," and suggested further interpretations of the completeness of the fossil record of any group as implied by the relative degree of congruence of its preserved fossil record with its phylogeny. One implication of Norell's analysis is that we should expect to find the earliest records of many groups pushed back in time, as we determine that their sister groups were already extant. Norell (1992) notes that although the earliest records of most lizard



*Figure 6* X and Y are sister taxa, and Z is their outgroup. The fossil record of X is older than that of Y, but the early presence of members of group X implies that members of group Y were also present then.

families do not predate the latest Cretaceous (Estes 1983), the lineages were separate by no later than the Early Cretaceous, according to cladistic analysis, and this has implications for the biogeographic spread of lizards (both before and after the breakup of Pangaea). Ghost lineages can be assumed to have existed, and in some cases can be counted as real, if unknown, taxa when dealing with some kinds of macroevolutionary problems. Much depends on the completeness of the stratigraphic record. Norell & Novacek (1992a,b) and Norell (1993) surveyed dozens of vertebrate groups, comparing known stratigraphic ranges with divergence patterns expected on the basis of cladistic phylogenies. They found highly variable patterns, depending as much on superpositional as on cladistic resolution (Figure 7). For example, if members of a group did not separate well stratigraphically, the phylogeny could not be expected to be recovered in this sequence. As Norell & Novacek (1992b) note, "a good fossil record is one that can be empirically demonstrated to contain evolutionary pattern, as opposed to information that only reflects preservational bias." Testing the fossil record against cladistic phylogenies determines how complete the record probably is, and therefore how useful the taxon might be for stratigraphic purposes.

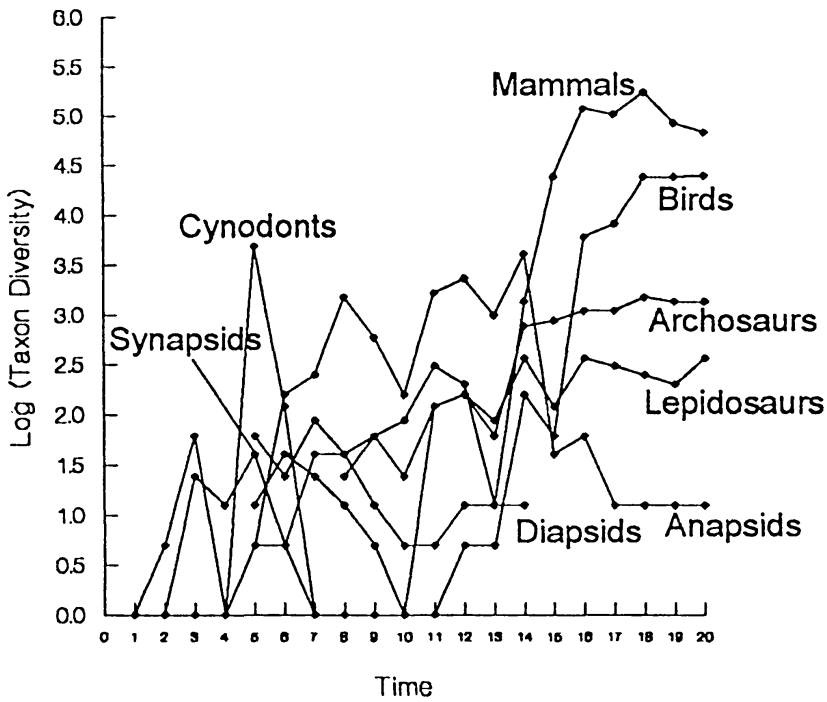
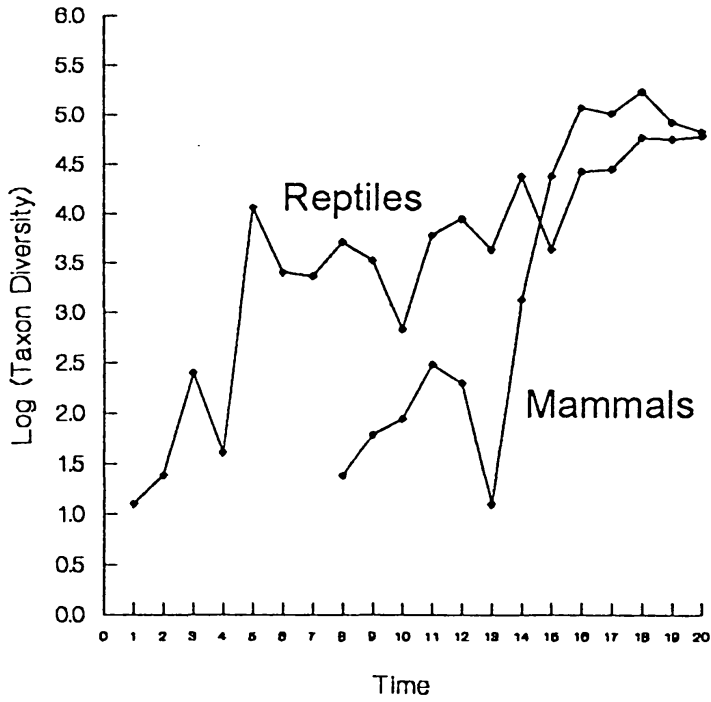
Beyond these considerations is the understanding of how the use of paraphyletic versus monophyletic groups affects our perception of biotic



*Figure 7* Clade rank versus age rank for the two major branches of amniotes—Synapsida and Diapsida. In this example the high degree of scatter in the diapsids indicates that the correlation between their phylogeny and the appearance of diapsid taxa in the fossil record is poor relative to the synapsids which show a higher correlation. After Norell & Novacek (1992b).

turnover. There seems to be general agreement among workers in all paleontological fields that traditional taxonomy does not reflect actual phylogenetic relationships very well. (If there are four “families” in an order, this says nothing about the relationship of these “families” to each other, or whether any or all are paraphyletic.) For some time, phylogeneticists have wondered whether the substantial portion of paraphyletic taxa in the fossil record could be giving misleading signals about the pace of diversity through time. Sepkoski & Kendrick (1991) modeled phylogenetic diversity with interesting results: They found that few changes were detectable in the major events of life through time when paraphyletic and monophyletic model clades were compared. But as one might expect, the fidelity of correspondence was higher at lower taxonomic levels. The signals for origination and extinction patterns were somewhat damped, compared to a paraphyletic pattern. Overall, however, Sepkoski & Kendrick found that traditional paraphyletic taxa can yield a meaningful signal, if sampling is sufficient. But these conclusions about model taxa have not been sustained by other workers studying actual data sets (Donoghue 1991, Smith & Patterson 1988, Archibald 1993, Edgecombe 1992).

An example of the importance of monophyletic groups to the assessment of patterns of biotic turnover through time can be readily provided by the history of tetrapods (Padian & Clemens 1985, Benton 1989a, Padian 1989b). As noted above in our first section, traditional classification holds that both mammals and birds evolved from (separate) “reptile” ancestors. Under this view, “reptiles” constitute a paraphyletic group. Cladistic revision of tetrapod groups, discussed above, instead focuses on the earliest amniotes, and restricts “reptiles” to living reptiles (including birds) and all taxa closer to them than to mammals. Under this view, the amniotes have two great branches, one leading to the living reptiles and birds (Reptilia or Sauropsida), and another leading to mammals and their relatives (Synapsida). This requires us to stop thinking about the extinct relatives of mammals as “reptiles.” If we do so, and plot the respective histories of these clades through time (Figure 8), we find that there has been something of a relay race between the two, with the synapsids predominant in the Late Paleozoic, the reptiles coming into prominence in the Late Triassic and dominating until the Late Cretaceous, and the synapsids again (in the form of mammals) surging in the Tertiary, as do the reptiles once more (in the form of birds, plus the lizards, snakes, crocodiles, and turtles). This is substantially different from the old division between the “Age of Reptiles” (the Mesozoic) and the “Age of Mammals” (the Cenozoic), which is more a reflection of which land animals were among the largest or most conspicuous at a particular time.





In protistan paleontology, stratigraphy and morphology provide the framework on which most systematic and evolutionary studies are done. This is not surprising given the relatively fine resolution that is attainable within samples. However, a strictly stratigraphic approach can lead to circular arguments regarding relationships. For example, the appearance of distinct morphological sequences through time, combined with the presence of possible morphological intergrades, is often interpreted as an evolutionary series connecting ancestral and derived taxa. How characters change is also determined from these sequences, and independent, non-stratigraphic evidence is wanting. It is neither sufficient nor robust to: (a) recognize a relationship between two morphologically similar taxa based on their sequence in the geological column, (b) describe the character transformations based on this sequence, and (c) then construct an evolutionary scenario to explain the change. While the protist fossil record is the best available, its resolution does not abrogate the need for independent assessment of the relationships among protist taxa.

Cladistic analyses of protists are beginning to appear in the literature (D'Hondt 1991, MacLeod 1988, MacLeod & Kitchell 1988), and recently these analyses have been used as hypotheses against which to test adaptational scenarios. MacLeod (1993) examined speciation events in the microfossil record using the Maastrichtian-Danian radiation of triserial and biserial planktic foraminifera. Although this event has been traditionally considered one of the best examples of adaptive radiation, MacLeod found that while there was congruence between patterns of morphological change and habitat shifts, speciation rates were higher than expected given the rates of habitat diversification. MacLeod therefore rejected the "vacant niche" model and considered the "taxon-pulse" model to be more plausible. Rigorous testing of these alternative models of

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*Figure 8* The top graph treats diversity through time (arbitrary units) by breaking amniotes into mammals and "reptiles," in which "reptiles" include all amniotes that aren't mammals (except birds, not pictured here). The bottom graph divides amniotes cladistically: Many former "reptiles" now group with the mammals in Synapsida, and birds are included in Reptilia. A "relay race" now becomes more apparent: Synapsids dominated the Permian and Early Triassic, but diapsids (mostly archosaurs) took over in the mid-Triassic and dominated until the Late Cretaceous extinctions. Turtles took up a small role in the Late Triassic and continue to the Recent; lizards and their relatives (lepidosaurs) maintained a low profile through the Mesozoic but lately their record has improved. Marine reptiles are mostly responsible for the Mesozoic diversity of diapsids apart from archosaurs and lepidosaurs. The synapsids resurged again in the Tertiary, but it cannot strictly be called the "Age of Mammals" because surviving reptiles, especially birds, constitute a considerable portion of Tertiary diversity.

speciation and adaptation were only possible because of the use of cladistic analysis.

### *Calibration of the Molecular Clock*

One of the most topical applications of cladistics in paleontology is to the question of rates of evolution, particularly molecular evolution. After molecular sequence data became available, first for proteins and later for DNA, it was noticed that rates of sequence divergence were so regular (Zuckerkandl & Pauling 1962, 1965; Margoliash 1963) that they could be used to estimate the time of divergence between two lineages. The relative constancy of molecular sequence evolution contradicted some previous assessments of evolutionary rates based on morphology preserved in the fossil record. Morphology is known to evolve at varying rates, in part with varying selection pressures (Simpson 1944, 1953). Sarich & Wilson (1967a,b) used fossils to put an absolute time scale on serum albumin evolution in Primates. They found that the tree of Primates based on immunological distances among the albumins corresponded to the accepted morphological tree of the primate groups they were studying. They calibrated the time of divergence between anthropoids and Old World monkeys at about 30 million years ago, based on fossil evidence, and they proportionally estimated the probable time of divergence between humans and other apes at about 5 million years ago. This age was much younger than that estimated by paleontologists at the time, but fossil evidence later corroborated a more recent divergence between hominids and other apes, although not as late as 5 million years ago (Pilbeam 1978, Greenfield 1980).

Current debates on molecular clocks question the constancy and group-specificity of the evolution of particular genes. Calibrations of some molecular clocks have been based on a few poorly controlled divergence dates from the fossil record. The timing of the Old World Monkey/anthropoid split is still controversial (Simons 1990), the timings of eubacteria divergences used to calibrate 16S rRNA have wide margins of error (Wilson et al 1987), and divergence times of rodent groups are also based on sketchy phylogenetic positions of fossils (Catzeflis et al 1992). Some early molecular phylogenies set divergence points at the first appearance of a group member in the fossil record; so, for example, the crocodile-bird split was calibrated by the first known crocodile (Late Triassic, about 210 my ago). But cladistic analysis shows that the crocodile-bird split occurred at least 235 my ago (Middle Triassic)—a 10% difference in calibration. Similarly, the first turtles appear in the Late Triassic (about 210 million years ago), but cladistic analysis shows that their lineage must have split from the other reptiles (their sister group, the Diapsida) at least by the Middle Pennsyl-

vanian (about 350 my ago)—a 50% difference in calibration. Fossil representatives of turtle sister groups are now beginning to fill this temporal gap (Gaffney 1980, Reisz & Laurin 1991).

To improve the utility of molecular clocks, comprehensive studies of extant taxonomic groups with excellent fossil records are necessary. The groups should have a variety of living representatives that have both shallow and deep branch-points in the group phylogeny, and there should be well dated fossil taxa associated with the nodes to provide minimum estimates of divergence times. Such data would provide a strict time control for comparing divergence rates amongst the lineages containing extant forms. Good examples of such groups include marine molluscs and mammalian carnivores, whose respectively long (about 550 my) and recent (about 50 my) fossil records could test slowly and rapidly evolving molecules, respectively.

### *The Evolution of Major Adaptations*

Historically, the evolution of major adaptations in the history of life has been treated by looking for “key innovations” in functional complexes that frequently characterize a diverse group, such as gastropods or mammals. Frequently, this approach has centered on identifying such key features and then devising an adaptive scenario to explain their evolution in terms of orthodox Darwinian natural selection (e.g. Bock 1986). However, this logic is circular and so is inherently incapable of testing any hypotheses about evolution (Padian 1994). Cladistic approaches to phylogeny provide an independent test of such hypotheses, because the methods of cladistics naturally separate the clusters of adaptive characters into a hierarchical sequence of acquisition. So, for example, as noted above, cladistic analysis has strongly supported the hypothesis that birds evolved from small carnivorous dinosaurs (Ostrom 1976; Padian 1982; Gauthier 1984, 1986). What does this tell us about the origins of flight, a major adaptation?

The theropod dinosaurs from which birds evolved already had a hand reduced to the first three fingers, a foot reduced to the middle three toes (with the first offset to the side), a long, S-shaped neck, and gracile hindlimbs with a long shank and reduced fibula. In the lineage leading to birds, the forelimbs increased in length, the tail shortened and stiffened slightly, and eventually the bones of the pelvis began to shift backwards while the hands grew longer and began to flex sideways (Padian 1982, Gauthier 1984, Gauthier & Padian 1985, Padian 1987). This sequence of evolution of features is available as an independent test of how flight evolved. For example, the view that birds were initially arboreal climbers that glided and eventually took active flight finds no support in the record of phylogeny (cf

Bock 1986). On the contrary, the inferred habits of bird relatives are terrestrial, cursorial, and predatory, which suggests an origin of flight from the ground up, by incremental running leaps (Padian 1987, 1994). Hypotheses of functional origin should be kept separate from phylogenetic hypotheses, so that they may be tested independently (Padian 1982, 1987, 1994). In this way the sequence of assembly of major adaptive complexes may be dissected, and the pattern of evolution is made available to test hypotheses of evolutionary process.

Gastropod molluscs are one of the most diverse groups of invertebrate animals, both in form and habitat. They have figured prominently in paleontological and biological studies, and have served as study organisms in numerous evolutionary, biomechanical, ecological, physiological, and behavioral studies. The higher classification of gastropods has received scant attention for much of this century but recently there has been a comprehensive reconsideration of gastropod phylogeny (e.g. Graham 1985, Haszprunar 1988). An increasing awareness of the importance of phylogeny in the construction of evolutionary scenarios and explanations requires a rigorous analysis of the data, so that alternative theories and interpretations of molluscan evolution can be evaluated.

For more than 70 years, gastropods have been divided into a tripartite classification scheme that correlates the abundance of various members of these groups with the divisions of the Phanerozoic. Thus, in the Paleozoic the Archaeogastropoda are the predominant group, and the Mesozoic is the age of the Mesogastropoda; during the Cenozoic the Neogastropoda become dominant. While these taxonomic divisions are often treated as clades in terms of adaptive prowess, ecological diversity, and so on, they are clearly grades of evolution and not clades that share exclusive ancestors. Moreover, members of these groups are all present in the fossil record by the end of the Paleozoic, and it is only differential turnover in taxonomic rates that produce the stratigraphically-stepped patterns of the groups. Like the patterns seen in the vertebrates (Figure 8), the use of gastropod clades rather than grades produces a more complex and interesting history for the group.

This is not to assert that questions asked about “grades” are always noninformational. For example, there may be questions about herbivory in gastropods that make little difference if asked cladistically; but *within* “herbivores” the kind of herbivory used, or the multiple evolutions of radiations and specializations, can only be revealed by phylogenetic analysis. In other words, a phylogenetic hypothesis may not be needed to measure or describe a taxon, its features, performance, interactions, etc. However, when one begins talking about how it got that way, a phylogenetic hypothesis is implicitly necessary (see also O’Hara 1988).

## *Biogeography*

In addition to temporal information, the fossil record also provides spatial patterns of taxa. Paleobiogeographic studies seek to document the changing distributions of animals and plants through time and correlate these changes with physical and biotic events and perturbations. Evolutionary scenarios to explain these disjunct distributions are moot if the “species pair” does not share a common ancestor. And what is meant by a region having “low generic diversity”? Are all genera created equal and therefore a comparable form of organismal currency? Clearly, these studies require independent assessment and demonstration of the phyletic relationships of the organisms.

Historically, changes in the distribution of organisms have been interpreted as the results of dispersal events (Forbes 1846, Darwin 1859, Depéret 1908, Matthew 1915). In the marine realm these changes were easily explained by the dispersal of pelagic larvae or rafted adults. Terrestrial taxa were more problematic: Fragmented distributions of taxa often required complex networks of land bridges between continents. The discovery and acceptance of plate tectonics in the late 1960s also sparked a revolution in biogeographic studies. Plants and animals now rode plates into new configurations rather than sauntered between them on mythical bridges. Plate tectonics provided a mechanism by which distributions could be both divided or connected. And again it was Gareth Nelson, and his colleagues, Donn Rosen and Norman Platnick at the American Museum of Natural History in New York, who championed the approach that has become known as vicariance biogeography (see Nelson & Platnick 1981).

Inherent in any biogeographic study are assumptions of relationship (e.g. gene flow among individuals of a population or common ancestry of taxa that compose a clade) (see Wiley 1981 for an overview). Whether a taxon has been divided or rafted into a new region via crustal plate segments or the water column, the “smoking gun” of such an event is the recognition of a relationship between the disjunct taxa. However, most taxa lack a modern phylogenetic treatment. Thus, sister taxa status (i.e. two taxa that share a common ancestor) has not been demonstrated for many of the classical examples cited in the literature. Instead of a phylogenetic hypotheses, most workers use the Linnean classification as a proxy for relatedness. However, there remains the danger of confusing common ancestry with convergence.

Although dispersal and vicariance are often cast as diametrically opposed processes, Hallam's (1981, p.340) point that vicariance and dispersal are “two sides of the same coin” appears to apply even within a single biotope. For example, while the closing of the Panamic portal produced a vicariance event that separated Caribbean and tropical eastern

Pacific marine organisms, the perturbations to tropical current patterns caused by the emerging isthmus appears to have facilitated the interchange of temperate marine organisms between the northeastern and southeastern Pacific Oceans (Lindberg 1991) as well as the great American vertebrate interchange (Stehli & Webb 1985).

Biogeographical patterns may be elucidated through the use of area cladograms. Like taxon cladograms, area cladograms also reflect relationships, albeit relationships between areas or regions. Figure 9 illustrates the relationships and the patterns of divergence between the major crustal plates. Taxa with relationships that are congruent with this area cladogram would not falsify a vicariance model of their biogeographic history. Moreover, the addition of fossils often provides critical resolution of area cladograms, especially in those situations where the taxon has become extinct in one or more areas.

Taxon and area cladograms, used in conjunction with fossil occurrences, can also provide support for the biogeographic history of dispersing marine invertebrates. Many marine gastropod and bivalve taxa of the northeastern Pacific Ocean have sister taxa with earlier geological occurrences in the northwestern Pacific (MacNeil 1965, Marinovich 1983, Vermeij 1991, and references therein). Some of these taxa are also present in the southeastern Pacific (Lindberg 1991). For several of these groups, taxon and area cladograms and the fossil record all support a dispersal history from the northwestern Pacific to the northeastern Pacific and subsequently into the southeastern Pacific (Figure 10).

Fossil horses are perhaps the most commonly used textbook story of evolution. They attracted the attention of early evolutionists because their history combined aspects of adaptation, morphological change, and biogeography in a single, familiar example demonstrating gradual evolu-

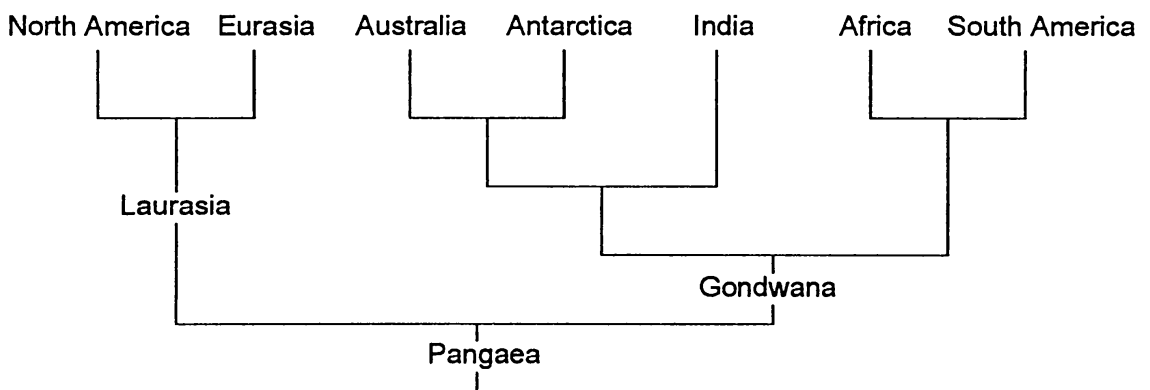
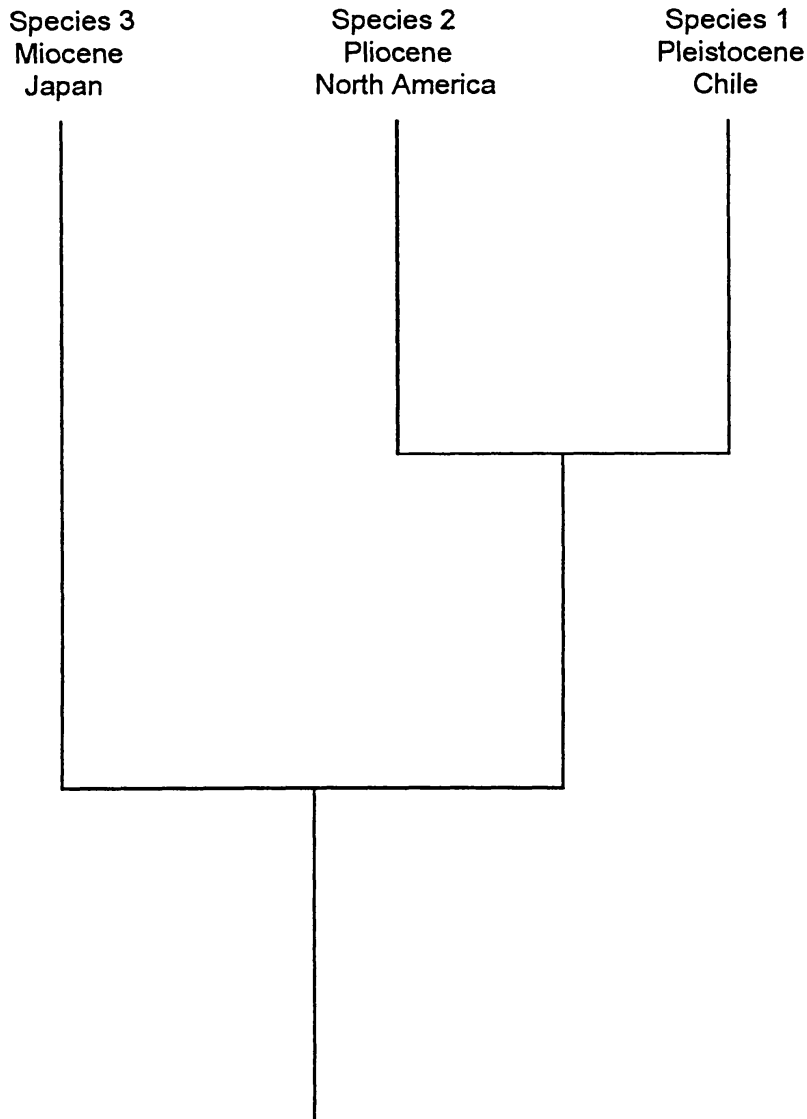


Figure 9 Area cladogram for the breaking up of Pangaea during the last 220 million years.



*Figure 10* Congruence of area and taxon cladograms for the dispersal of a nearshore marine gastropod taxon from the northwestern Pacific → northeastern Pacific → southeastern Pacific during the Tertiary. The first fossil occurrence of the taxon in each region is also congruent with these relationships. See Lindberg (1991) for examples.

tionary change through time. They had a small, short-faced, five-toed ancestor with a low-crowned dentition suited for browsing, but as climates changed and grasslands appeared during the Miocene, the number of toes was gradually reduced and the teeth became higher crowned and more useful for grazing and grinding grass. Pre-cladistic analyses of horse phylogeny and biogeography indicated that horses originated in North America, with *Hyracotherium* (“Eohippus”), and that they dispersed on four sep-

arate occasions to the Old World via the Bering Bridge during the late Cenozoic and once to South America via Panama during the Pleistocene (Simpson 1951). Cladistic analyses of horse relationships (Hooker 1989; Hulbert 1989; MacFadden 1976, 1992) have shown that, while essentially correct, horse evolution and biogeography are considerably more complicated than previously thought. MacFadden (1992) argues that while the horse family (Equidae) may have originated in North America if their closest relatives were the Eocene Phenacodontidae, it is also possible that they were related to *Radinskya* from Asia. If the latter is the case, then equids must have immigrated to North America from Asia. Cladistic analyses also show that equids underwent a vicariant event (i.e. their group naturally divided geographically) in the mid-Eocene, when the DeGeer land bridge between North America and Scandinavia broke apart (MacFadden 1992). As a result, the true "equidae" were isolated in North America and the Palaeotheriidae were isolated in Eurasia. Following the rupture of the DeGeer bridge, the Bering bridge became the dominant route of dispersal for horses. By plotting the geographic and stratigraphic occurrences of equids on a cladogram of their relationships it is possible to reconstruct four major dispersals of equids out of North America. The early hyracotheres emigrated in the Eocene, the Anchitheres emigrated in the early Miocene, the Hipparions in the late Miocene, and the true horses in the Plio-Pleistocene (MacFadden 1992). Only by having a detailed knowledge of horse relationships is it possible to reconstruct the history of their migrations and evolution in all of its complexity.

## CONCLUSIONS

Cladistics has revolutionized the way we look at historical biology, or what has traditionally been called "evolution." Cladistics elucidates the patterns of evolution by forcing scientists to state explicitly and hierarchically the evidence that appears to link biological taxa to other taxa. This method is far more exposed to direct evaluation than are the methods of traditional evolutionary biology. Scientists cannot simply invoke Darwin and hide behind assertions of adaptive value or necessary selective pressures; instead, they must first demonstrate the patterns shown by the characteristics of the organisms. Hypotheses about evolutionary processes can then be evaluated against the evolutionary patterns revealed by the organisms themselves.

We have tried to show how cladistic analysis of the pattern of biological history works as a starting point for the analysis of other patterns, such as biogeographic history, and processes, such as the evolution of major adaptive features. Cladistics is an endpoint in historical biology only when



investigators are interested in nothing further than the most parsimonious evaluation of relationships among groups. While important, this function leaves unexplored the power of cladistic analysis to approach broader evolutionary problems.

In this equation, the role of fossils is complex and has sometimes been underestimated. Because fossils are necessarily less complete than living organisms, they preserve only a portion of their original information. Nonetheless, to ignore fossils, or to treat them simply as taxa that should be “added later” to historical analyses based on living forms, is a mistake, as several studies have shown (Donoghue et al 1989). Gauthier et al (1988a) showed that if certain early extinct taxa related to mammals are omitted from phylogenetic analysis, mammals and birds show up as sister groups (to the exclusion of crocodiles and other reptiles), or birds and crocodiles are the sister group of mammals (to the exclusion of turtles and lizards). Doyle & Donoghue (1987) showed that without including the extinct taxa *Caytonia* and the Bennettitales, some crucial features in angiosperm plant evolution could not be recovered accurately and the polarity of some characters would be reversed at certain hierarchical levels. From these examples it can easily be seen that cladistic analysis constrains certain kinds of scenarios in historical biology—not just of the evolution of characters and groups, but of their adaptive features, their biogeography, and the vicissitudes of their diversity through time.

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#### Literature Cited

- Archibald JD. 1993. The importance of phylogenetic analysis for the assessment of species turnover: a case history of Paleocene mammals in North America. *Paleobiology* 19: 1–27
- Benton MJ, ed. 1988. *Phylogeny and Classification of the Tetrapods*, Vols. 1, 2. Oxford: Clarendon. 377 pp. 329 pp.
- Benton MJ. 1989a. Patterns of evolution and extinction in vertebrates. In *Evolution and the Fossil Record*, ed. KC Allen, DEG Briggs, pp. 218–41. London: Belhaven
- Benton MJ. 1989b. Mass extinctions among tetrapods and the quality of the fossil record. *Phil. Trans. R. Soc. London Ser. B* 325: 369–86
- Benton MJ, Clark JM. 1988. Archosaur phylogeny and the relationships of the Crocodylia. See Benton 1988, Vol. 1, pp. 289–332
- Bock WJ. 1986. The arboreal origin of avian flight. In *The Origin of Birds and the Evolution of Flight*, ed. K Padian, pp. 57–82. *Mem. Calif. Acad. Sci.* 8

- Briggs DEG, Fortey RA. 1989. The early radiation and relationships of the major Arthropod groups. *Science* 246: 241–43
- Briggs DEG, Fortey RA, Wills MA. 1992. Morphological disparity in the Cambrian. *Science* 256: 1670–73
- Brooks DJ, McLennan DA. 1990. *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. Chicago: Univ. Chicago Press. 434 pp.
- Carroll RL. 1988. *Vertebrate Paleontology and Evolution*. New York: Freeman. 698 pp.
- Catzefflis FM, Aguilar J, Jaeger J-J. 1992. Muroid rodents, phylogeny and evolution. *Trends Ecol. Evol.* 7(4): 122–26
- Cracraft J. 1988. The major clades of birds. See Benton 1988, Vol. 1, pp. 339–61
- Darwin C. 1859. *On the Origin of Species by Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray
- Depéret C. 1908. The evolution of Tertiary mammals, and the importance of their migrations. *Amer. N.* 42(494): 109–14, (495): 166–70, (497): 303–7
- de Queiroz K. 1987. Phylogenetic systematics of iguanine lizards: a comparative study. *Univ. Calif. Publ. Zool.* 118: 1–203
- de Queiroz K, Gauthier J. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Syst. Zool.* 39: 307–22
- de Queiroz K, Gauthier J. 1992. Phylogenetic taxonomy. *Annu. Rev. Ecol. Syst.* 23: 449–80
- D'Hondt S. 1991. Phylogenetic and stratigraphic analysis of earliest Paleocene biserial and triserial planktonic foraminifera. *J. Foraminiferal Res.* 21: 168–81
- Donoghue MJ. 1991. The use of phylogenies in studying diversification, with examples from plants. *Geol. Soc. Am. Abstr. Prog.* 23: A281 (Abstr.)
- Donoghue MJ, Doyle JA, Gauthier J, Kluge AG, Rowe T. 1989. The importance of fossils in phylogeny reconstruction. *Annu. Rev. Ecol. Syst.* 20: 431–60
- Doyle JA, Donoghue MJ. 1987. The importance of fossils in elucidating seed plant phylogeny and macroevolution. *Rev. Palaeobot. Palynol.* 53: 321–431
- Edgecombe GD. 1992. Trilobite phylogeny and the Cambrian-Ordovician "Event": Cladistic reappraisal. In *Extinction and Phylogeny*, ed. MJ Novacek, QD Wheeler, pp. 144–177. New York: Columbia Univ. Press
- Eldredge N, Cracraft J. 1980. *Phylogenetic Patterns and the Evolutionary Process*. New York: Columbia Univ. Press. 349 pp.
- Estes R. 1983. Sauria terrestria, Amphibia. *Handbuch der Palaeoherpetologie*, Vol. 10A. Stuttgart: Gustav Fischer
- Estes R, Pregill G, eds. 1988. *Phylogenetic Relationships of Lizard Families*. Palo Alto, CA: Stanford Univ. Press. 631 pp.
- Evans SE. 1988. The early history and relationships of the Diapsida. See Benton 1988, Vol. 1, pp. 221–60
- Farris JS. 1988. HENNIG86. Version 1.5. Computer program distributed by author: 41 Admiral St., Port Jefferson Station, NY
- Felsenstein J. 1991. *PHYLIP*. Phylogeny Inference Package Ver. 3.4. Seattle: Univ. Washington
- Footo M, Gould SJ. 1992. Cambrian and Recent morphological disparity. *Science* 258: 1816
- Forbes E 1846. On the connexion between the distribution of the existing fauna and flora of the British Isles, and the geological changes which have affected their area especially during the epoch of the great northern drift. *Mem. Geol. Surv. Great Britain* 1: 336–432
- Frost DR, Etheridge R. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Misc. Publ. Univ. Kansas Mus. Nat. Hist.* 81: 1–65
- Gaffney ES. 1980. Tetrapod monophyly: a phylogenetic analysis. *Bull. Carnegie Mus. Nat. Hist.* 13: 92–105
- Gauthier JA. 1984. *A cladistic analysis of the higher systematic categories of the Diapsida*. PhD Thesis. Univ. Calif., Berkeley
- Gauthier JA. 1986. Saurischian monophyly and the origin of birds. In *The Origin of Birds and the Evolution of Flight*, ed. K Padian, pp. 1–55. *Mem. Calif. Acad. Sci.* 8
- Gauthier JA, Cannatella D, de Queiroz K, Kluge AG, Rowe T. 1989. Tetrapod phylogeny. In *The Hierarchy of Life*, ed. B Fernholm, K Bremer, H Jornvall, 25: 337–53. Amsterdam: Elsevier. 499 pp.
- Gauthier J, Estes R, de Queiroz K. 1988. A phylogenetic analysis of Lepidosauromorpha. See Estes & Pregill 1988, pp. 15–99
- Gauthier JA, Kluge AG, Rowe T. 1988a. Amniote Phylogeny and the importance of fossils. *Cladistics* 4: 105–209
- Gauthier JA, Kluge AG, Rowe T. 1988b. The early evolution of the Amniota. See Benton 1988, Vol. 1, pp. 103–56
- Gauthier J, Padian K. 1985. Phylogenetic, functional, and aerodynamic hypotheses

- of the origin of birds and their flight. In *The Beginnings of Birds*, ed. MK Hecht, JH Ostrom, G Viohl, P Wellnhofer, pp. 185–97. Eichstatt, Germany: Freunde des JuraMuseums. 382 pp.
- Gould SJ. 1989. *Wonderful Life: The Burgess Shale and the Nature of History*. New York: Norton. 347 pp.
- Gould SJ. 1991. The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: Why we must strive to quantify morphospace. *Paleobiology* 17(4): 411–23
- Graham A. 1985. Evolution within the Gastropoda: Prosobranchia. In *The Mollusca Evolution*, ed. ER Trueman, MR Clark, 10: 151–86. New York: Academic
- Greenfield LO. 1980. A late divergence hypothesis. *Am. J. Phys. Anthropol.* 52: 351–65
- Hallam A. 1981. Response. In *Vicariance Biogeography: A Critique*, ed. G Nelson, D Rosen, p. 340. New York: Columbia Univ. Press
- Harvey PH, Pagel MD. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford Univ. Press. 239 pp.
- Haszprunar G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura (Mollusca). *J. Moll. Stud.* 54: 367–441
- Heaton MJ. 1980. The Cotylosauria: a reconsideration of a group of archaic tetrapods. See Panchen 1980, pp. 497–552
- Hennig W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag
- Hennig W. 1966. *Phylogenetic Systematics*. Urbana: Univ. Ill. Press. 263 pp.
- Hooker JJ. 1989. Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. See Prothero & Schoch 1989, pp. 79–101
- Hulbert RC Jr. 1989. Phylogenetic interrelationships and evolution of North American late Neogene Equidae. See Prothero & Schoch 1989, pp. 176–96
- Hull DL. 1988. *Science as a Process*. Chicago: Univ. Chicago Press
- Knight JB. 1952. Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Misc. Coll.* 117(13): 1–56
- Lindberg DR. 1991. Marine biotic interchange between the northern and southern hemispheres. *Paleobiology* 17(3): 308–24
- MacFadden BJ. 1976. Cladistic analysis of primitive equids, with notes on other perissodactyls. *Syst. Zool.* 25: 1–14
- MacFadden BJ. 1992. *Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equidae*. Cambridge: Cambridge Univ. Press. 369 pp.
- MacLeod N. 1988. Lower and middle Jurassic *Perispyridium* (Radiolaria) from the Snowshoe Formation, east-central Oregon. *Micropaleontology* 34: 289–315
- MacLeod N. 1993. The Maastrichtian-Danian radiation of triserial and biserial planktic foraminifera: testing phylogenetic and adaptational hypotheses in the (micro) fossil record. *Mar. Micropaleontol.* 21: 47–100
- MacLeod N, Kitchell, JA. 1988. The origin of *Hantkenina*: a phylogenetic analysis of alternative hypotheses. *Geol. Soc. Am. Abstr. Progr.* 20(6): A228 (Abstr.)
- MacNeil FS. 1965. Evolution and distribution of the genus *Mya*, and Tertiary migrations of Mollusca. *U.S. Geol. Surv. Prof. Pap.* 483-G: 1–51
- Maddison WP, Donoghue MJ, Maddison DR. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33: 83–103
- Maddison WP, Maddison DR. 1992. *MacClade: Analysis of Phylogeny and Character Evolution. Version 3.0*. Sunderland, England: Sinauer Assoc.
- Margoliash E. 1963. Primary structure and evolution of cytochrome c. *Proc. Natl. Acad. Sci. USA* 50: 672–79
- Marincovich L Jr. 1983. Molluscan paleontology, paleoecology, and North Pacific correlations of the Miocene Tacxhilni Formation, Alaska Peninsula, Alaska. *Bull. Am. Paleontol.* 84(317): 1–155
- Matthew WD. 1915. Climate and evolution. *Ann. New York Acad. Sci.* 24: 171–318
- McKenna MC. 1987. Molecular and morphological analysis of high-level mammalian interrelationships. See Patterson 1987, pp. 55–93
- Milner AR. 1988. The relationships and origin of living amphibians. See Benton 1988, pp. 59–102
- Nelson GJ, Platnick NI. 1981. *Cladistics and Vicariance: Patterns in Comparative Biology*. New York: Columbia Univ. Press
- Norell MA. 1992. Taxic origin and temporal diversity: the effect of phylogeny. In *Phylogeny and Extinction*, ed. MJ Novacek, QD Wheeler, pp. 89–118. New York: Columbia Univ. Press
- Norell MA. 1993. Tree-based approaches to understanding history: comments on ranks, rules, and the quality of the fossil record. *Am. J. Sci.* 293-A: 407–17
- Norell MA, Novacek MJ. 1992a. The fossil record: comparing cladistic and paleontological evidence for vertebrate history. *Science* 255: 1690–93

- Norell MA, Novacek MJ. 1992b. Congruence between superpositional and phylogenetic patterns: comparing cladistic patterns with fossil records. *Cladistics* 8: 319–38
- Novacek MJ. 1992. Mammalian phylogeny: shaking the tree. *Nature* 356: 121–25
- Novacek MJ, Wyss AR. 1986. Higher-level relationships of the recent Eutherian orders: morphological evidence. *Cladistics* 2: 257–87
- O'Hara RJ. 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. *Syst. Zool.* 37(2): 142–55
- Ostrom JH. 1976. *Archaeopteryx* and the origin of birds. *Biol. J. Linn. Soc.* 8: 91–182
- Padian K. 1982. Macroevolution and the origin of major adaptations: vertebrate flight as a paradigm for the analysis of patterns. *Proc. Third. N. Am. Paleontol. Conv.* 2: 387–92
- Padian K. 1987. A comparative phylogenetic and functional approach to the origin of vertebrate flight. In *Recent Advances in the Study of Bats*, ed. B Fenton, PA Pacey, JMV Rayner, pp. 3–22. Cambridge: Cambridge Univ. Press
- Padian K. 1989a. Did “thecodontians” survive the Triassic? In *Dawn of the Age of Dinosaurs in the American Southwest*, ed. SG Lucas, AP Hunt, pp. 401–14. Albuquerque: New Mex. Mus. Nat. Hist.
- Padian K. 1989b. Rebounds and relays in vertebrate evolution. *Geol. Soc. Am. Abstr. Prog.* 21: A31 (Abstr.)
- Padian K. 1994. Form vs. Function: the evolution of a dialectic. In *Functional Morphology and Vertebrate Paleontology*, ed. JJ Thomason. Cambridge: Cambridge Univ. Press
- Padian, K., Clemens, W.A. 1985. Terrestrial vertebrate diversity: episodes and insights. In *Phanerozoic Diversity Patterns*, ed. J.W. Valentine, pp. 41–96. Princeton: Princeton Univ. Press. 441 pp.
- Panchen AL. 1980. *The Terrestrial Environment and the Origin of Land Vertebrates*. London: Academic. 633 pp.
- Panchen AL, Smithson TR. 1988. The relationships of the earliest tetrapods. See Benton 1988, Vol. 1, pp. 1–32
- Patterson C. 1987. *Molecules and Morphology in Evolution: Conflict or Compromise?* Cambridge: Cambridge Univ. Press. 229 pp.
- Perle A, Norell MA, Chiappe LM, Clark JM. 1993. Flightless bird from the Cretaceous of Mongolia. *Nature* 362: 623–28
- Pilbeam DR. 1978. Rethinking human origins. *Discovery* 13(1): 2–9
- Prothero DR, Schoch RM. 1989. *The Evolution of Perissodactyls*. Oxford: Clarendon. 537 pp.
- Reisz R, Laurin M. 1991. *Owenetta* and the origin of turtles. *Nature* 349: 324–26
- Rieppel O. 1988. The classification of the Squamata. See Benton 1988, Vol. 1, pp. 261–94
- Rowe T. 1987. Definition and diagnosis in the phylogenetic system. *Syst. Zool.* 36: 208–11
- Sarich VM, Wilson AC. 1967a. Rates of albumin evolution in Primates. *Proc. Natl. Acad. Sci. USA* 58: 142–47
- Sarich VM, Wilson AC. 1967b. Immunological time scale for hominid evolution. *Science* 158: 1200–4
- Sepkoski JJ, Kendrick DC. 1991. Numerical experiments with model paraphyletic taxa. *Geol. Soc. Am. Abstr. Prog.* 23: A281 (Abstr.)
- Sereno PC. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *Natl. Geogr. Soc. Res.* 2: 234–56
- Sereno PC. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Mem. Soc. Vert. Paleontol.* 2: 1–53
- Sereno PC, Rao C. 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. *Science* 255: 845–48
- Simons E.L. 1990. Discovery of the oldest known anthropoidean skull from the Paleogene of Egypt. *Science* 237: 1567–69
- Simpson GG. 1944. *Tempo and Mode in Evolution*. New York: Columbia Univ. Press. 237 pp.
- Simpson GG. 1951. *Horses: The Story of the Horse Family in the Modern World and through Sixty Million Years of History*. New York: Oxford Univ. Press. 247 pp.
- Simpson GG. 1953. *The Major Features of Evolution*. New York: Columbia Univ. Press. 434 pp.
- Smith AB, Patterson C. 1988. The influence of taxonomic method on the perception of patterns of evolution. *Evol. Biol.* 23: 127–216
- Stehli FG, Webb SD. 1985. *The Great American Biotic Interchange*. New York: Plenum
- Stuber, RA, Lindberg DR. 1989. Is the raddula of living monoplacophorans primitive? *Geol. Soc. Am. Abstr. Prog.* 21(7): A289 (Abstr.)
- Swofford DL. 1991. *PAUP: Phylogenetic Analysis Using Parsimony*. Version 3.1. Computer program distributed by Ill. Nat. Hist. Surv., Champaign, Ill
- Vermeij GJ. 1991. When biotas meet—understanding biotic interchange. *Science* 253: 1099–104

- Wiley EO. 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. New York: Wiley-Interscience. 439 pp.
- Wiley EO, Siegel-Causey D, Brooks DR, Funk VA. 1991. The complete cladist: A primer of phylogenetic procedures. *Univ. Kans. Spec. Publ.* 19: 1-158
- Wilson AC, Ochman H, Prager EM. 1987. Molecular time scale for evolution. *Trends Genet.* 3: 241-47
- Zuckerkindl E, Pauling L. 1962. Molecular disease, evolution, and genetic diversity. In *Horizons in Biochemistry*, ed. M Kasha, B Pullman, pp. 189-225. New York: Academic
- Zuckerkindl E, Pauling L. 1965. Evolutionary divergence and convergence in proteins. In *Evolving Genes and Proteins*, ed. V Bryson, HJ Vogel, pp. 97-166. New York: Academic