

PROGRESS AND FUTURE DIRECTIONS IN ARCHOSAUR PHYLOGENETICS

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ABSTRACT—The basic structure of archosaurian phylogeny is understood to include two primary crown-group lineages—one leading to living crocodyles and including a broad diversity of Triassic animals (e.g., phytosaurs, rauisuchians, aetosaurs), and another leading to dinosaurs (living and extinct). These lineages were established by the middle Triassic. A few extinct groups remain controversial, such as the pterosaurs, and debate persists over the phylogenetic relationships among extant bird lineages, which have proved difficult to resolve, and divergence timing estimates within Aves and Crocodylia remain the source of contention. A few analyses support a close relationship between archosaurs and turtles, or even a nesting of turtles within Archosauria. All sources of information used to resolve these issues have weaknesses, and these problems all involve highly derived lineages when they first appear in the fossil record.

ARCHOSAURS, REPRESENTED today by birds and crocodylians, are only a minor fragment of the total scope of living and extinct biodiversity. They are dwarfed in diversity and abundance by the arthropods and flowering plants that truly own the planet, and even among vertebrates the bony fish are much more diverse (Wilson, 1988). But archosaurs adopt a disproportionately large role in lay considerations of biology and paleontology. We see birds every day and find them attractive. And nonavian dinosaurs bring instant recognition and capture the imagination.

Archosaurs have arguably played a pivotal role in the history of paleontology and phylogenetics. Early dinosaur discoveries created a sensation in the 19th century, and the fevered rush to collect giant dinosaurs for museums, led to the discovery of several important fossil localities around the world, many of which are still productive (Colbert, 1968; Desmond, 1982; Cadbury, 2000; McGowan, 2001). The scientific study of archosaurs has seen a resurgence over the past three or four decades, driven by new discoveries, by new analytical techniques, and by a more sophisticated scientific philosophy centered as much on important questions as on the intrinsic allure of the animals themselves. Because most people find dinosaurs (living and extinct) appealing, new discoveries and surrounding controversies often find their way to the broadcast media. Dinosaurs and their relatives can be seen as ambassadors of science to the general public (e.g., Padian, 1992).

Modern phylogenetic systematics was first brought to vertebrate paleontology by students of fossil fish, but its application to archosaurs showed the power of a phylogenetic approach to the broader community. Pioneering phylogenetic surveys in the 1980s laid out the general framework of archosaurian relationships and confirmed growing suspicions that birds are derived theropod dinosaurs (Gauthier, 1984, 1986; Benton, 1984; Gauthier and Padian, 1985; Benton and Clark, 1988; Sereno and Arcucci, 1990). When added to a broader data set for amniotes (Gauthier et al., 1988), these helped demonstrate the central role fossils could play in phylogeny reconstruction. Attention to phylogeny has characterized studies of archosaur historical biogeography (e.g., Wilson and Sereno, 1998; Sereno, 2000; Cracraft, 2001), functional evolution (e.g., Gatesy and Middleton, 1997; Carrano, 1998; Carrier and Farmer, 2000; Hutchinson, 2001a, 2001b), developmental biology (Larsson, 1998), and paleobiology (e.g., Varricchio et al., 1999; Horner et al., 1999; Erickson and Brochu, 2000).

The purpose of this paper is to review current understanding of archosaur phylogenetics and to indicate the questions that, in this author's view, present the next set of challenges archosaur systematists face. Archosaurs have a rich fossil record, but also include living members. Despite the sampling of diverse sources of data, from skeletal anatomy to nucleic acid sequences, and

despite the expanded methodological toolbox available to the systematist, some portions of the archosaur tree resist resolution. Phylogenetic relationships among crown-group bird "orders" are perhaps the most significant of these. We also encounter interesting conflicts between fossil and molecular data sets regarding lineage divergence timing within both birds and crocodylians, and at least some sequence-based analyses argue that turtles belong within Archosauria. These challenges lie at the interface between paleontology and neontology.

ARCHOSAUR RELATIONSHIPS—WHERE WE AGREE (USUALLY)

Archosauria was one of the first groups for which phylogeny-based taxon names were applied (Gauthier, 1984, 1986; Gauthier and Padian, 1985; Benton and Clark, 1988). In phylogenetic nomenclature, taxon name definitions are based on ancestry and descent rather than the possession of subjective "key" characters (de Quieroz and Gauthier, 1990, 1992; Cantino and de Quieroz, 2000). Phylogenetic name definitions will be used throughout this paper.

Archosauria, as defined by Gauthier and Padian (1985) and based on Gauthier's (1984, 1986) pioneering work, is defined in reference to the last common ancestor of birds and crocodylians and all of its descendants. Crown-group Archosauria excludes a few animals previously classified as archosaurs that possessed what were thought to be the hallmark features of the group—socketed teeth and an antorbital fenestra. The name Archosauriformes was erected for Archosauria sensu lato—Archosauria, Proterosuchidae, Proterochampsidae, *Euparkeria*, and Erythrosuchidae (Fig. 1). The term "Thecodontia" refers to the paraphyletic assemblage of archosauriforms not belonging to Crocodyliformes, Dinosauria, or Pterosauria (Gauthier and Padian, 1985) and is not considered a taxon name. Some authors continue to use Archosauria in its prephylogenetic sense (e.g., Benton, 1999; Gower, 2000), and in this sense taxonomy is *not* one of the issues on which archosaur systematists agree. However, nomenclatural issues are neither as important nor as interesting as conflicts over the data itself.

Archosauriformes is part of a much broader clade named Archosauromorpha, which is defined on the basis of crocodylians, birds, and all taxa more closely related to them than to lepidosaurs. This group includes a bizarre assemblage of predominantly Triassic forms, such as trilophosaurids, rhynchosaurs, and proterosaurians (Gauthier et al., 1988; Renesto, 1994; de Braga and Rieppel, 1997; Merck, 1997; Dilkes, 1998; Peters, 2000). The non-archosauriform relationships in Figure 1 are derived primarily from Merck (1997).

The placement of champsosaurs (Choristodera) within Archosauromorpha was controversial at first, because the group was

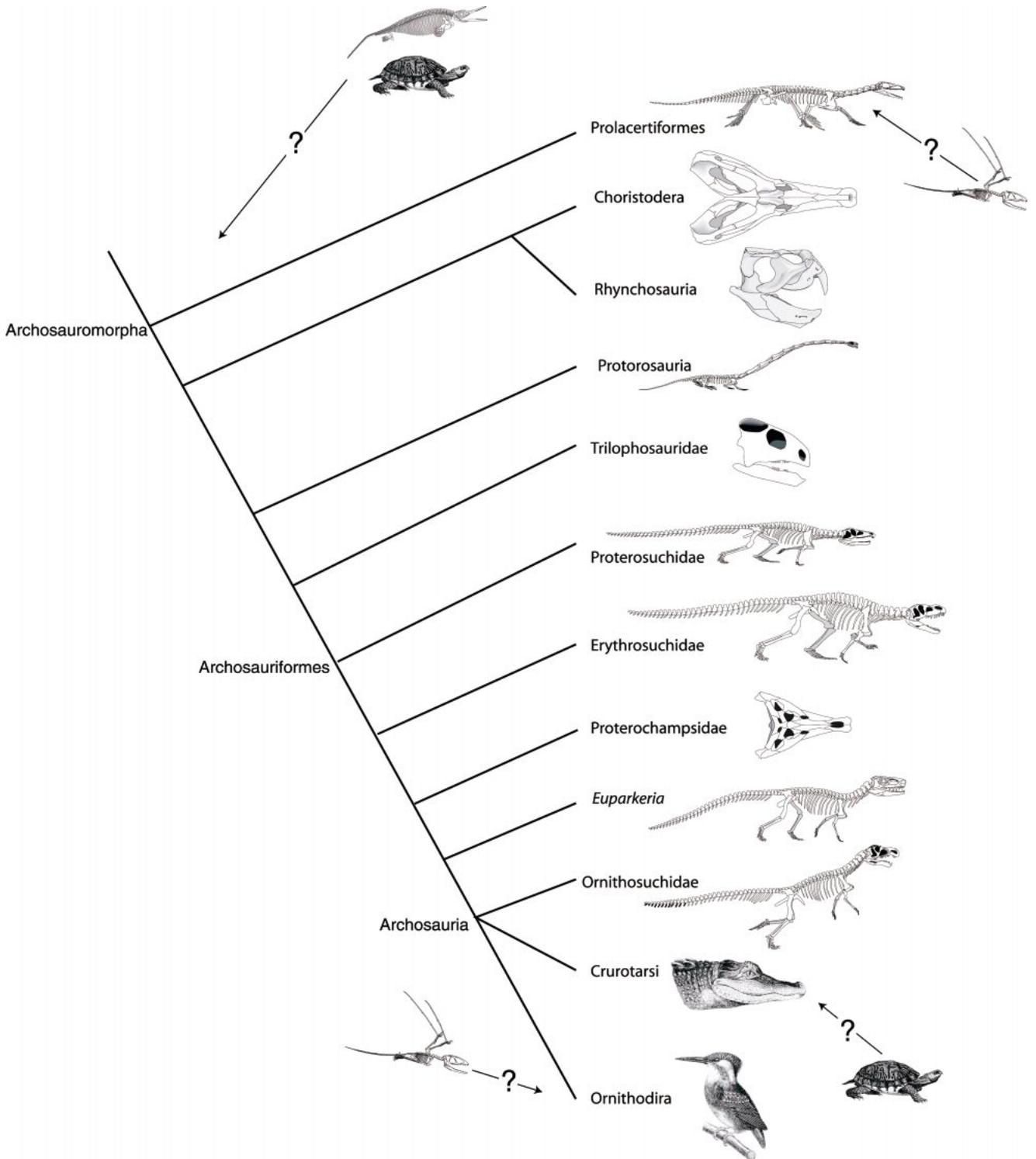


FIGURE 1—Phylogenetic relationships among archosauromorphs based on recent analyses. See text for discussion.

until recently known only from the Late Cretaceous through Tertiary (Evans and Hecht, 1993). A rootward position within Archosauromorpha implies an unsampled history minimally into the Triassic, where choristodere sister taxa appear. Putative choristoderes were subsequently identified from Jurassic and Late Triassic deposits (Evans, 1989, 1991; Storrs and Gower, 1993).

Sister groups to Archosauria are first known from relatively complete material in the Early Triassic, although one probable proterosuchid is known from the Late Permian of Russia (Tatarinov, 1960; Gower and Sennikov, 2000). With the exception of the Permian occurrence, the proterosuchids and erythrosuchids are restricted to the Early and Middle Triassic (Gower and Sennikov, 1997,

2000). Proterochampsids are found in Late Triassic (Carnian) units of South America (Reig, 1959; Sill, 1967; Romer, 1972). These were quadrupedal carnivores with a powerful bite, as evidenced by the socketed, serrated teeth and enlarged attachment space for the jaw adductors and trigeminal musculature. They also bear an antorbital fenestra, the function of which remains unclear (Witmer, 1997). The largest non-archosaur archosauriforms had half-meter-long skulls. Detailed anatomical and taxonomic reviews of these taxa can be found in Walker (1964), Parrish (1992), Gower and Sennikov (1997, 2000), Gower and Weber (1998), and Welman (1998).

The oldest-known crown-group archosaurs are Anisian “rauisuchians.” The interrelationships and monophyly of Rauisuchia remain controversial (Gower, 2000), but there is general agreement that “rauisuchians,” broadly conceived, are more closely related to crocodylians than to birds (Benton and Clark, 1988; Sereno and Arcucci, 1990; Sereno, 1991a; Parrish, 1993; Juul, 1994; Gower and Wilkinson, 1996). Other crown-group archosaurian forms are first known from fossils in the Ladinian (Benton, 1995).

Most analyses agree that Parasuchia (phytosaur), Aetosauria, and the various “rauisuchian” lineages are close relatives of Crocodylomorpha (Gauthier, 1986; Benton and Clark, 1989; Sereno and Arcucci, 1990; Sereno, 1991a; Parrish, 1993; Juul, 1994; Gower and Wilkinson, 1996; Fig. 2). All of these animals (pseudosuchians) have a so-called “crocodile-normal” ankle, with a rotary ankle joint in which the proximal tarsals (astragalus and calcaneum) move against each other with a peg-and-socket articulation. In these taxa, the peg is on the astragalus and the socket on the calcaneum. Whether the “crocodile-reversed” archosaurs (ornithosuchids, where the peg is on the calcaneum and socket on the astragalus) are related to crocodylians (Sereno, 1991a; Parrish, 1993) or closer to dinosauromorphs with plesiomorphic mesotarsal articulations (Gauthier, 1986; Juul, 1994) is a matter of controversy, but the difference is one or two nodes. Cruickshank (1979), Sereno (1991a), Parrish (1986, 1993), Gower (1996), and Dyke (1998) provide valuable reviews of archosaur ankle morphology and phylogenetic relevance.

There is similar consensus on the close relationship between *Scleromochlus*, *Marasuchus*, *Pseudolagosuchus*, *Lagerpeton*, and Dinosauria (Gauthier, 1986; Sereno, 1991a; Sereno and Arcucci, 1994a, 1994b; Novas, 1996; Benton, 1999a; Fig. 3). Pterosaurs are usually regarded as members of this assemblage, but some recent reviews argue against their archosaurian affinities (see below).

The ancestral archosaur was a predator that could probably locomote on two or four legs. It also probably had several soft-tissue and behavioral features known in extant archosaurs, such as a four-chambered heart and at least some degree of nest building and parental care (Gauthier et al., 1988). The basalmost pseudosuchians remained quadrupedal and robustly built, but basal dinosauromorphs show a tendency to lengthen the hindlimb relative to the body and to have more gracile limb proportions.

The only pseudosuchian lineage to survive the Triassic is Crocodylomorpha, which includes an assemblage of gracile “sphenosuchians” (the monophyly of which is debated, e.g., Benton and Clark, 1988; Walker, 1990; Sereno and Wild, 1992; Wu and Chatterjee, 1993; Clark et al., 2000) and crocodyliiforms. Crocodyliiformes includes those animals conventionally called “crocodylians” in the prephylogenetic literature, though the term “crocodylian” is now restricted to the crown group. Crocodyliiformes was traditionally grouped into a series of three grades—Protosuchia, Mesosuchia, and Eusuchia—on the basis of palate and vertebral morphology (e.g., Langston, 1973; Buffetaut, 1982), but of these, only Eusuchia is demonstrably monophyletic (Benton and Clark, 1988; Brochu, 1997; Buscalioni et al., 2001). The earliest eusuchian is *Hylaeochampsia vectiana* from the Early Cretaceous of

England (Clark and Norell, 1992); there are scattered putative eusuchian occurrences throughout the Cretaceous (Stromer, 1925, 1933; Efimov, 1982), and the first crown-group crocodylians appear in the Campanian (Erickson, 1972; Wu et al., 1996; Williamson, 1996).

Crocodylian phylogenetics in Figure 2 are summarized from Brochu (1997), Salisbury and Willis (1996), and Buscalioni et al. (2001) and reflect the morphological perspective on gavialoid relationships. For the most part, molecular and morphological data agree rather strongly on the details of crocodylian phylogeny—Alligatoridae is monophyletic and *Crocodylus*, *Osteolaemus*, and *Tomistoma* are more closely related to each other than any are to Alligatoridae (Poe, 1996; Brochu and Densmore, 2001). There is even broad agreement on divergence timing estimates, with notable exceptions (see below).

Dinosaurian monophyly is supported by virtually all phylogenetic analyses of Archosauria. Herrerasaurids and *Eoraptor* may be outside Dinosauria or basal theropods (Gauthier, 1986; Brinkman and Sues, 1987; Novas, 1992, 1994; Padian and May, 1993; Sereno, 1993, 1999; Sereno and Novas, 1993; Holtz and Padian, 1995; Galton, 1999; Holtz, 2000), but the earliest dinosaurian fossils include primitive sauropodomorphs and ornithischians (Sereno, 1991b; Flynn et al., 1999). The primary branches of Dinosauria were thus distinct by the Carnian.

The ancestral dinosaur was an enhancement of the morphology seen in nondinosaurian dinosauromorphs such as *Marasuchus*. It was probably a bipedal animal, probably predatory, and probably the size of a large dog. Early ornithischians and sauropodomorphs already show modifications for herbivory, but basal members of these clades remained small and bipedal (Sereno, 1991b; Benton et al., 2000). The ancestral archosaur was very likely able to keep the belly off the ground by rotating the hindlimb into a vertical orientation during locomotion, a mode of walking seen frequently in living crocodylians (Gatesy, 1991). The ancestral dinosaur took this a step further by forcing its hindlimbs under the body with an inturned femoral head, constraining hindlimb movement to the parasagittal plane. These modifications are thought to reflect a decoupling of breathing and walking and to permit breathing while running, something the ancestral diapsid could not do (Carrier, 1991; Carrier and Farmer, 2000).

Various aspects of dinosaurian relationships might appear contentious to the casual observer, especially when they are discussed in public. In fact, the different hypotheses are highly congruent (Holtz, 1999). Figures 3 and 4 summarize much of the work over the past decade (Gauthier, 1986; Holtz, 1994, 2000; Sues, 1997; Forster et al., 1998; Makovicky and Sues, 1998; Sereno, 1999, 2001; Currie and Carpenter, 2000; Norell et al., 2001; Chiappe, 2001), with particular attention to the theropods. Additional work discussing relationships within the terminal taxa shown in Figure 3 can be found in Sereno (1986, 1991b), Weishampel et al. (1990), Forster (1990, 1997), Upchurch (1995), Currie and Padian (1997), Wilson and Sereno (1998), Chinnery and Weishampel (1998), Head (1998), and Makovicky (2001).

One of the more interesting resolutions in recent years is that therezinosauroids, or segnosaur, are highly modified theropods. The segnosaurian skull preserves a confusing mixture of ornithischian, sauropodomorph, and theropod features, and it was difficult to figure out what these animals were (Perle, 1979, 1982; Gauthier, 1986). New material described in the 1990s (Russell and Dong, 1993; Clark et al., 1994; Xu et al., 1999) firmly establishes them as theropods. The only remaining controversy is whether therezinosauroids are closer to ornithomimosaurs (Sereno, 1999) or to oviraptorosaurs (Holtz, 2000; Norell et al., 2001).

That birds are derived theropod dinosaurs is no longer the subject of scholarly dispute. Every phylogenetic analysis conducted on archosaur relationships supports this conclusion (Gauthier,

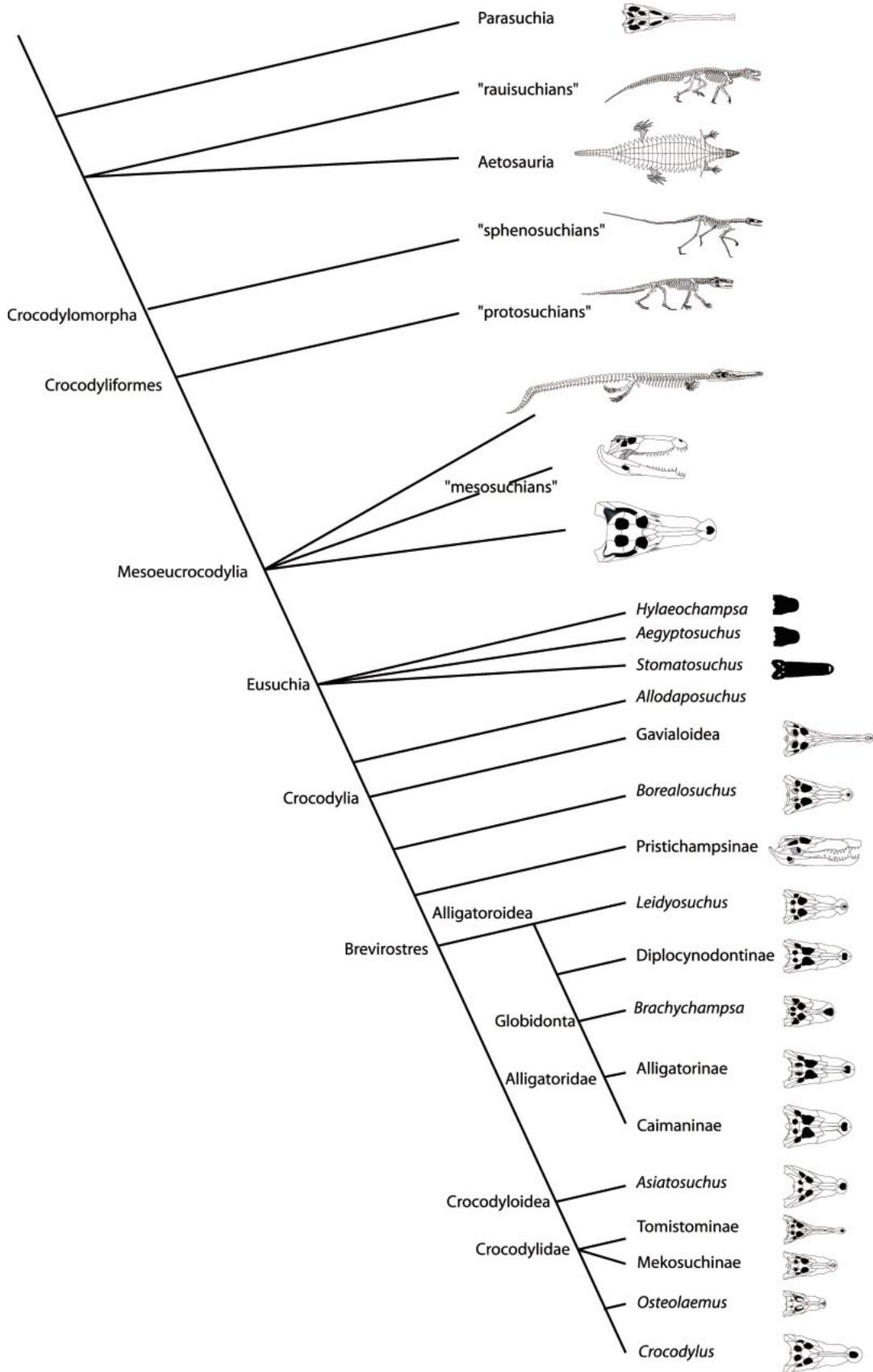


FIGURE 2—Phylogenetic relationships among crocodylomorph archosaurs based on recent analyses. See text for discussion.

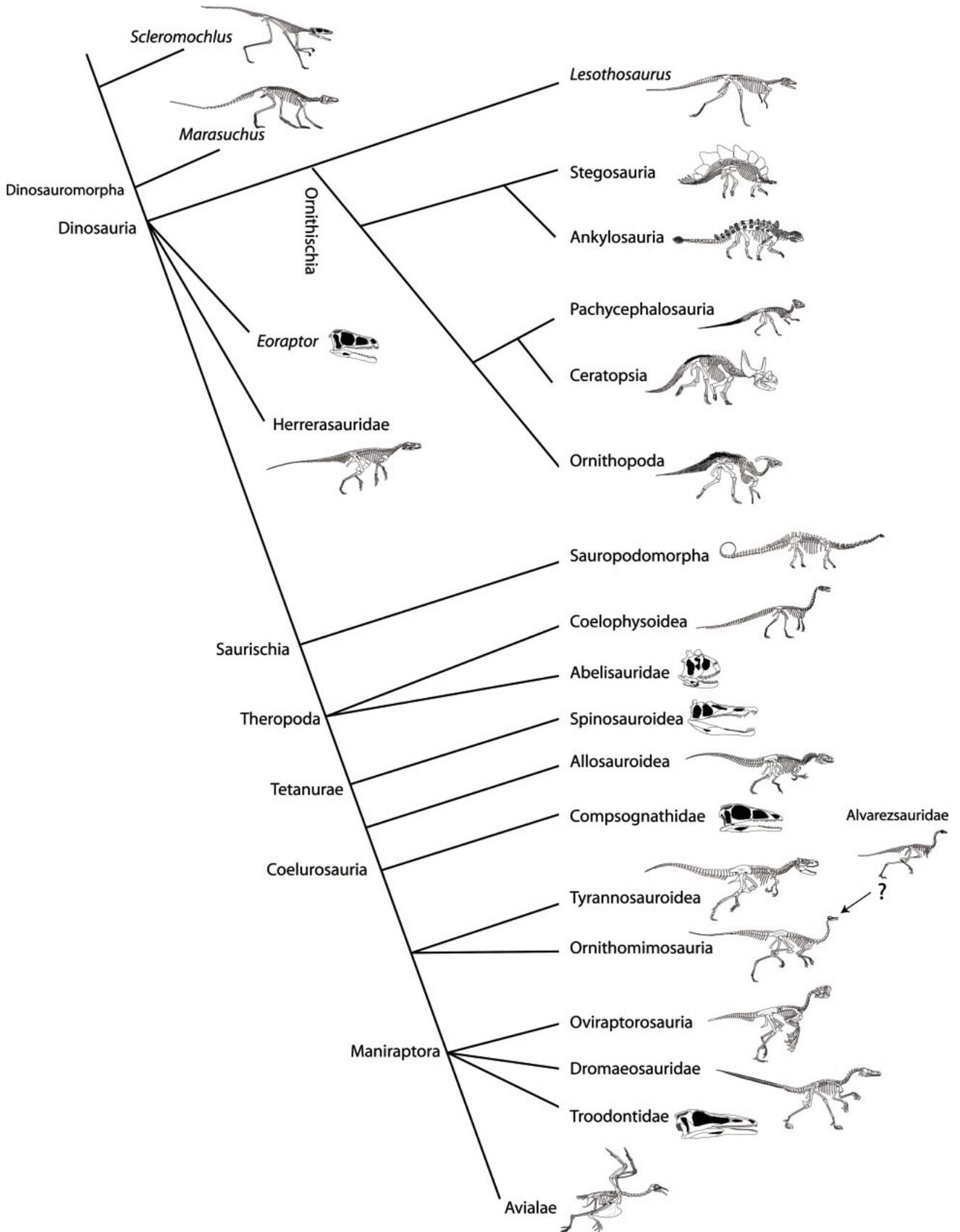


FIGURE 3—Phylogenetic relationships among dinosaurs based on recent analyses. See text for discussion.

1986; Benton and Clark, 1988; Holtz, 1994, 2000; Novas and Pueria, 1997; Padian and Chiappe, 1998; Forster et al., 1998; Chiappe et al., 1998; Chatterjee, 1999; Sereno, 1999; Norell et al., 2001), and arguments to the contrary are rhetorical more than evidential (Padian, 2001). The recent discovery of nonavian theropods with apparent feathers or featherlike structures in north-eastern China (Chen et al., 1998; Xu et al., 1999, 2000, 2001; Ji et al., 1998, 2001) confirms this as tightly as the idea that humans are derived primates or that fruit flies are derived arthropods. The only real controversy over basal bird relationships involves the bizarre alvarezsaurids, which were first thought to be highly modified flightless birds (Perle et al., 1994; Novas, 1996; Chiappe et al., 1996, 1998), but which subsequent analyses suggest may be outside Avialae, though closely related to it (Holtz, 2000; Norell et al., 2001; Chiappe, 2001), or close relatives of ornithomimosaurs (Sereno, 1999, 2001).

The name Aves, as applied in this paper, is the crown group including the last common ancestor of paleognaths and neognaths (the two extant bird lineages) and all of its descendants. This particular application of Aves is not universally accepted, and some authorities use Neornithes for the crown group (e.g., Craft, 2001). The name Avialae refers to the stem-based group including Aves (or Neornithes) and all theropods closer to it than to the dromaeosaurid *Deinonychus* (Padian et al., 1999).

The earliest fossil that everyone agrees is a bird is *Archaeopteryx* from the Tithonian of Germany. But the meaning of "bird" has become ambiguous (Padian, 1998; Padian and Chiappe, 1998; Hutchinson, 2001a). An exercise I often use in my classes involves mapping the various features popularly thought to distinguish birds from other living vertebrates—feathers, toothless beak, "bird foot," reduced tail, fused wrist and ankle, wishbone, and so on—on a cladogram of archosaurian relationships. I then ask where the transition from nonbird to bird lies. Very few characters actually diagnose Avialae relative to other theropods. Most "bird" characters either appear further down the tree (including feathers) or diagnose subsets of Avialae. This can be a powerful way to demonstrate evolution—the students literally "see" birds arise on the blackboard.

The number of known bird fossils from the Mesozoic has skyrocketed in the past 15 yr (Chiappe, 1997). Most of these have been referred to Enantiornithes (e.g., Walker, 1988; Sanz et al., 1995; Chiappe, 1995; Martin, 1995; Hou et al., 1996; Zhang and Zhou, 2000), but one recent study questions the monophyly of this group (Norell and Clarke, 2001). By the end of the Cretaceous, birds were geographically widespread and morphologically diverse, though the relative impact of the Cretaceous-Tertiary extinction event on birds is debated (see below).

Most (but not all) studies support a monophyletic Paleognathae (the familiar flightless ratites and volant tinamous), but this has been historically controversial (Feduccia, 1996). Relationships within Neognathae are virtually unresolved (see below), but most (though not all) data sets support the basal position of a monophyletic Galloanserae, a clade including galliforms (chickens and relatives) and anseriforms (waterfowl).

ARCHOSAUR RELATIONSHIPS—WHERE WE DISAGREE

Euryapsids and Turtles.—Ichthyosaurs and sauropterygians (plesiosaurs, placodonts, and nothosaurs) were marine reptiles restricted to the Mesozoic. These forms share the possession of a single upper temporal fenestra (the "euryapsid" condition), and they were frequently classified together as members of Euryapsida. For much of the 20th century, they were regarded as very basal amniotes. But by the 1980's, euryapsid monophyly was no longer presumed and little could be said about the relationships of these animals within Amniota (e.g., Carroll, 1988). Because the highly derived skeletons of these secondarily aquatic forms

defied homology assessment, early cladistic surveys of amniote relationships generally excluded them (Gauthier et al., 1988; Lee, 1995; Laurin and Reisz, 1996).

De Braga and Rieppel (1997) and Rieppel and Reisz (1999) included sauropterygians in a phylogenetic analysis of reptiles. They came to the surprising conclusion that sauropterygians were very basal relatives of the lepidosaurs. Sauropterygians were thus derived diapsids, and the euryapsid condition with a single temporal fenestra was derived from the diapsid two-fenestra pattern. An analysis by Merck (1997) went a step further by including ichthyosaurs as well as sauropterygians. His analysis supported euryapsid monophyly and the diapsid affinities of marine reptiles, but Euryapsida was a basal archosauromorph lineage in his analysis, as tentatively shown in Figure 1. Whether inclusion of ichthyosaurs changes the results of Rieppel's analysis depends on the version of the matrix used (Rieppel and Reisz, 1999).

Even more surprising, inclusion of euryapsids drew turtles within Diapsida in both sets of studies. Turtles reflect the ancestral "anapsid" condition and lack temporal fenestration. For this reason, turtles have historically been regarded as "primitive" reptiles lying outside Diapsida, and all previous morphology-based cladistic analyses agreed that turtles were the living sister taxon of Diapsida (Gauthier et al., 1988; Laurin and Reisz, 1996; Lee, 1995, 1997a, 1997b). Turtles were seen as close relatives of sauropterygians (or even members of Sauropterygia) in the analyses including euryapsids; without euryapsids, those matrices support nondiapsid affinities for turtles.

This was not an entirely "new" conclusion, as anatomists of the late 19th and early 20th centuries sometimes made similar suggestions, but the characters used to draw this conclusion were later considered convergent (Gregory, 1946). It remains controversial within the phylogenetics community, and authors of papers supporting this conclusion acknowledge its heterodoxy (Rieppel and Reisz, 1999). The codings used in these analyses have been contested (e.g., Lee, 1997a), and a sauropterygian-chelonian relationship is weakly supported and based on characters that are homoplastic on the tree as a whole (Rieppel and Reisz, 1999). From a morphological perspective, this is a hypothesis clearly in need of further exploration.

Adding to the controversy, several independent molecular analyses also regard turtles as diapsids (Zardoya and Meyer, 2001). Mitochondrial sequence data argue for a clade that includes turtles, crocodylians, and birds to the exclusion of lepidosaurs, regardless of method (Platz and Conlon, 1997; Zardoya and Meyer, 1998; Janke et al., 2001). Nuclear genes have been less precise (e.g., Gorr et al., 1998), and some actually support a crocodylian-turtle clade to the exclusion of birds (Hedges and Poling, 1999; Mannen and Li, 1999), making turtles members of Archosauria in the restricted sense.

Although the molecular evidence for diapsid (and possibly archosaurian) affinities of turtles is compelling, it is not problem-free. Most importantly, we are working with ingroup divergences minimally older than the Jurassic, and available outgroups—mammals and lissamphibians—had diverged from the ingroup by the early Carboniferous. Furthermore, some of these genes show strong rate heterogeneity, which may be influencing the ingroup signal (Gorr et al., 1998). But not all genes show evidence for evolutionary rate heterogeneity, and none of these trees can be rerooted to make a "standard" tree with turtles outside Diapsida.

Another potential problem with these studies is taxon sampling. Most analyses include a single turtle, one or two birds (usually a neognath), one or two lepidosaurs, and a single crocodylian. This last point is interesting because the sole crocodylian is usually *Alligator mississippiensis*. Mitochondrial rates in crocodylians seem to be higher than in other reptiles (Kumazawa and Nishida, 1995; Quinn and Mindell, 1996; Janke et al., 2001), and for at

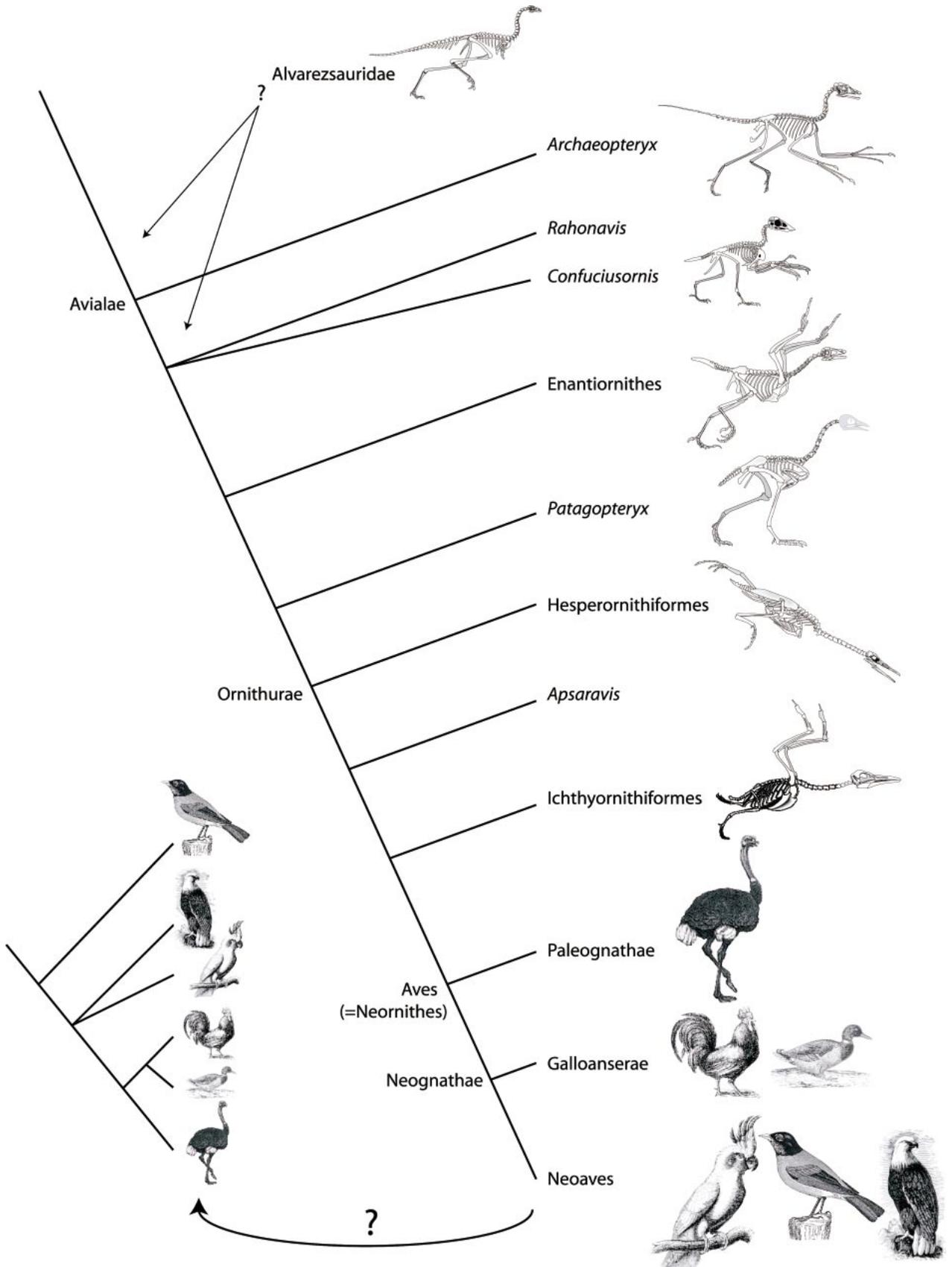


FIGURE 4—Phylogenetic relationships among birds based on recent analyses. Inset tree at lower left indicates alternative rooting for crown-group birds based on mitochondrial data. See text for discussion.

least some genes, rates are higher in alligatorids than in nonalligatorid crocodylians (Brochu, 1997). It would be interesting to reanalyze some of these sequences with some other crocodylian, or even with multiple crocodylians, as was done by Gorr et al. (1998). Switching to nuclear genes may not solve this problem entirely, as high rates and within-group rate variability have been reported for squamates (Hughes and Mouchiroud, 2001).

It would be easy to dismiss the molecular analyses as being misled by sequence saturation, a long-branch attraction problem, inadequate ingroup sampling, or by any other standard retort. The turtle-archosaur hypothesis is unsettling whether the supporting data are osteological or molecular. But similar questions can be raised about the morphological data brought to bear on this question. Turtles and sauropterygians are very derived when they first appear in the fossil record, and selecting a taxon to polarize morphological character states for them is problematic. More importantly, we might regard the "turtle question" as a matter of taxon sampling. Turtles are outside Diapsida when euryapsids are not included, but diapsids when they are.

As with many in the systematics community, I am skeptical that turtles are derived diapsids. But resolution of this conflict rests with new fossil discoveries, more detailed anatomical descriptions, and more thorough sampling of both taxa and genes. Hypotheses should be overturned on the basis of new evidence and not the counterintuitive appearance of the hypothesis itself.

Pterosaurian relationships.—Pterosaurs are the earliest known flying vertebrates and first appear in the Norian (Benton, 1995). They radiated extensively throughout the Mesozoic and include the largest flying animals known (Kellner and Langston, 1996). The earliest pterosaurs had toothy jaws and long tails; by the Late Cretaceous, the derived pterosaurs (pterodactyls) had reduced tails, toothless beaks, and often sported bizarre crests on the beak or cranium (Wellnhofer, 1991).

Most cladistic analyses regard pterosaurs as archosaurs closer to birds than to crocodylians, although they universally reject the notion that pterosaurs and birds both evolved from a common flying ancestor (Gauthier, 1986; Sereno, 1991). There has been some controversy whether pterosaurs are related to *Scleromochlus taylori*, a small archosaur from the Carnian of England (Padian, 1984; Gauthier, 1986; Sereno, 1991) or not (Benton, 1999), but the topological difference between these scenarios is rather modest.

Bennett (1996) argued that most of the characters supporting a close pterosaur-dinosauriform relationship were hindlimb features correlated with locomotion and thus not independent. Removal of these characters resulted in a tree with pterosaurs lying outside the clade including Archosauria, Erythrosuchidae, and Proterochampsidae. Although his arguments of functional relationship between some characters have merit, there is a difference between functional linkage and phylogenetic dependence. Characters can be phylogenetically independent and not covary on a cladogram, and yet still be functionally correlated. Most of the characters correlated with flight in birds, for example, did not arise at the same phylogenetic level—they can be regarded as functionally related, but phylogenetically independent. There is also the problem of determining functional linkage, especially in groups such as pterosaurs that are extinct (and thus unable to function). Although we must remain vigilant in our efforts to apply independent characters in phylogenetic analysis, nonindependence should be established on the basis of character covariation on a tree.

A more recent analysis by Peters (2000) is interesting because it draws pterosaurs out of Archosauriformes entirely and supports a close relationship between pterosaurs and prolacertiforms, a group of small Triassic reptiles. He argued that many of the characters linking pterosaurs and archosauriforms in other analyses

were actually present (convergently) in prolacertiforms or absent in pterosaurs. He also reconsidered the morphology of several Triassic prolacertiforms—most notably *Cosesaurus*, *Longisquama*, and *Sharovipteryx*. *Cosesaurus* and *Longisquama* have been implicated in the origin of birds by some authors, especially those who continue to argue against the dinosaurian origin of the group (Feduccia, 1996). Most recently, the unusual long scales preserved on *Longisquama* have been interpreted as actual feathers (Jones et al., 2000), though most authorities dispute that interpretation (Reisz and Sues, 2000; Prum et al., 2001). *Sharovipteryx* is a strange animal with what appears to be a membrane of skin stretched between the hindlimbs and tail. Some pterosaurs may have had a similar structure (Unwin and Bakhurina, 1994).

Peters' hypothesis is interesting, but is limited by the quality of preservation of some of the prolacertiforms forming the basis of his argument. Many are flattened or preserved as natural molds, and in many cases they are best studied with low-angle light casting shadows on the slab. Many of the characters discussed by Peters can be given multiple interpretations. Not all are convinced, for example, that *Longisquama* had an antorbital fenestra (Unwin et al., 2000; Unwin and Benton, 2001). Resolution of this conflict awaits collection of fossils that allow less ambiguous interpretation.

Slender-Snouted Crocodyliforms.—Snout shape varies systematically within Crocodylia, and a handful of basic head shapes appear to have arisen multiple times independently within Crocodylia and throughout Crocodyliformes (Busbey, 1994; Brochu, 2001). Five living species—*Gavialis gangeticus*, *Tomistoma schlegelii*, and three species of *Crocodylus*—have extremely slender snouts. A slender snout is usually viewed as an adaptation for catching fish (Langston, 1973), although ecological information for some of the extant forms with this snout morphology is lacking.

The number of times this type of snout evolved within the crown group depends on how one resolves the placement of *Gavialis* (see below), but it minimally arose five times independently. Similar snouts are found in various non-crocodylian crocodyliforms, such as the dyrosaurids, pholidosaurs, and thalattosuchians. Thalattosuchians and pholidosaurs are restricted to the Jurassic and Cretaceous, but dyrosaurids survived until the Eocene. These have historically been viewed as representing independent derivations of slender-snouted morphology separate from those within the crown group (Kälin, 1955; Buffetaut, 1982).

The earliest cladistic analyses of Crocodyliformes seemed to confirm this view—thalattosuchians were one of the basalmost members of Mesoeucrocodylia, and dyrosaurids were more closely related to Crocodylia (Benton and Clark, 1988; Norell and Clark, 1990). But more recent studies found support for a clade including the three non-eusuchian slender snouted lineages (Clark, 1994; Wu et al., 1997). This was regarded as very surprising, and the first analysis to suggest this result—that of Clark (1994)—expressed at least some suspicion that these groups were being drawn together by a suite of nonindependent characters linked to elongation of the snout. But when characters presumed to be correlated with longirostry were eliminated from the analysis, the same result was obtained (Clark, 1994). In effect, the pholidosaurids and dyrosaurids are drawing thalattosuchians crownward; when pholidosaurids and dyrosaurids are excluded from the matrix, thalattosuchians return to their expected position at the root of Mesoeucrocodylia (Buckley and Brochu, 1999).

In my view, two scenarios are involved. First, the analyses supporting this conclusion were conducted at a very high taxonomic level, including taxa from the Triassic through the Cenozoic. A great deal of anatomical detail could not be included in

those studies. It is very possible that inclusion of more morphological information from throughout the skeleton will support independent derivations of slender snout morphology in crocodyliforms. Second, these data sets may be accurately reflecting phylogeny, and our previous suppositions of snout evolution in crocodyliforms may have been mistaken.

Because we cannot actually *know* the true phylogeny, deciding between these scenarios will be difficult. Resolution of this issue will require further examination of fossil crocodyliforms and inclusion of a larger number of morphological characters, especially from regions of the skeleton not directly involved in snout shape.

Gavialis.—Because two of the key players in this story are slender-snouted crocodylians (*Gavialis* and *Tomistoma*), one is tempted to regard this as part of the “longsnout problem” in crocodyliform systematics. In fact, it represents two distinct points of disagreement between morphological and molecular data (Fig. 5). One is topological—morphological data have historically regarded *Gavialis* as the sister taxon to all other living crocodylians (Kälin, 1955; Tarsitano et al., 1989; Norell, 1989; Brochu, 1997), but most molecular data sets support a sister group relationship between *Gavialis* and *Tomistoma* (Densmore, 1983; Densmore and Owen, 1989; Densmore and White, 1991; Gatesy and Amato, 1992; Hass et al., 1993; White and Densmore, 2001). The other is temporal—did *Gavialis* diverge from its closest living relatives (whatever they are) in the Mesozoic, as paleontologists have long argued (Kälin, 1955), or did it last share a common ancestor with another living crocodylian in the Late Tertiary (Densmore and Dessauer, 1984; Hass et al., 1993)?

This is an unusual case of temporal conflict. Most of the celebrated disputes, such as the origins of metazoans or divergence of modern mammal and bird lineages (see below), involve molecular divergence estimates much older than those supported by the fossil record. One can either invoke an imprecise molecular clock or incomplete fossil record to reconcile the dispute, and since both are likely involved, the “dispute” is between expectations more than the data sets themselves. In this case, the molecular divergence estimate is much younger than what fossils indicate. Some protein distance information suggested a divergence as recently as ten million years ago between *Gavialis* and *Tomistoma* (Densmore and Dessauer, 1984), but the most recent phylogenetic analyses of fossil crocodylians strongly indicate a first appearance for Gavialoidea in the Campanian and Tomistominae in the Ypresian (Brochu, 1997). Ghost lineages cannot account for this disparity. This is all the more confounding when one considers the robust agreement between fossils and molecules on nearly every other aspect of crocodylian divergence timing, from the ancient split between alligators and caimans at or near the Cretaceous-Tertiary boundary to the post-Oligocene divergence among extant *Crocodylus* (Brochu, 2000; Brochu and Densmore, 2001). Something very peculiar is clearly going on.

Some recent work suggests that the topological difference may not be as profound as previously thought. It is true that various distance methods and sequence data, when analyzed using maximum unweighted parsimony, support a “standard” molecular topology that cannot be rerooted to support the “standard” morphology tree (Fig. 5). But when some mitochondrial genes are analyzed using weighted parsimony or maximum likelihood, the result is a topology consistent with morphology, albeit with a rooting on alligatorids rather than *Gavialis* (White and Densmore, 2001). These sequences also support a *Gavialis-Tomistoma* divergence in the Eocene—not as old as fossils indicate, but older than the Miocene divergence suggested previously.

This debate is still very much open. More genes are being sequenced and analyzed, both from mitochondrial and nuclear sources, and the trees they support are yet to be published. Further examination of the molecular evidence is warranted, and it is very

much premature to conclude that molecular data now support the morphological pattern. But a similar reexamination of the morphological evidence is necessary.

One of our limitations as paleontologists is taxon sampling—and this is ironic, because morphologists can include the fossils that outnumber living species five to one. The earliest known gavialoids, such as *Thoracosaurus*, already have the derived slender snout characteristic of extant *Gavialis*. The same is true for the basalmost tomistomines, which are only slightly different from other Eocene crocodyloids. Nodal support for Gavialoidea is rather high, but one wonders if this simply reflects the long unsampled history for the group; high nodal support in morphology can reflect a large number of diagnostic characters, which can be correlated with long stratigraphic gaps (Sidor and Hopson, 1998).

Just as with the more general crocodyliform longsnout problem, we are left to wonder if the snout-related characters diagnosing Gavialoidea and Tomistominae are independent. Not all support for these groups is concentrated in the rostrum, but much of it is (Brochu, 1997; Trueman, 1999). Furthermore, some fossil slender-snouted crocodylians have yet to be incorporated into the analysis, and there is a rather long stratigraphic void in the eusuchian record between *Hylaeochampsia* in the Barremian and the earliest crown-group crocodylians in the Campanian (Brochu, 2001). Sampling for crocodylians is similarly poor (though not entirely barren) in the Paleocene and Oligocene, at least relative to the latest Cretaceous and Eocene. We cannot assume that the sample currently available will reflect the signal supported by a larger sample should new discoveries be made in the future.

Crown-group bird relationships.—For extant birds, the Linnean “order” seems to have served the same functional purpose served by the “phylum” at the metazoan level—it expresses the boundary between (mostly) uncontested monophyly and unresolved relationships. No one questions the monophyly of Piciformes (woodpeckers and allies) or Apodiformes (swifts and hummingbirds), but determining how piciforms and apodiforms are related to other bird “orders” is another matter. This problem persists to this day.

A similar problem faces mammal systematists, and similar explanations have been given for both problems—most commonly, that birds and mammals underwent rapid bursts of diversification early in their histories, leaving few transitional fossils that would tie lineages together and leaving long branches connected by short internodes. Whether these bursts occurred before or after the Cretaceous-Tertiary boundary is a complex issue itself (see below), but is independent of our inability to recover a robust, universally-accepted hypothesis of relationships within crown-group Aves.

There is broad (though not universal) agreement that the paleognaths—living ratites and tinamous—form a clade. This has long been a controversial idea; some authorities thought the characters shared in common by ratites were convergences related to flightlessness, and the palate morphology shared by ratites and tinamous was argued to be plesiomorphic (Olson, 1985; Feduccia, 1996). The Gondwanan distribution of these animals was also problematic if one assumed a Tertiary divergence, as the ranges of different extant ratite species are separated by marine barriers that would favor aerial dispersal, thus implying a flying ancestor and multiple derivations of flightlessness (Feduccia, 1996). Parsimony analyses of morphology (Cracraft, 1974, 2001; Lee et al., 1997) and multiple molecular data sets (Sibley and Ahlquist, 1990; Lee et al., 1997; Härlid et al., 1998; van Tuinen et al., 2000) support ratite and paleognath monophyly, although the interrelationships within the group remain unclear.

Whether Paleognathae is the sister group to a monophyletic Neognathae is less certain. Morphology and some molecular data

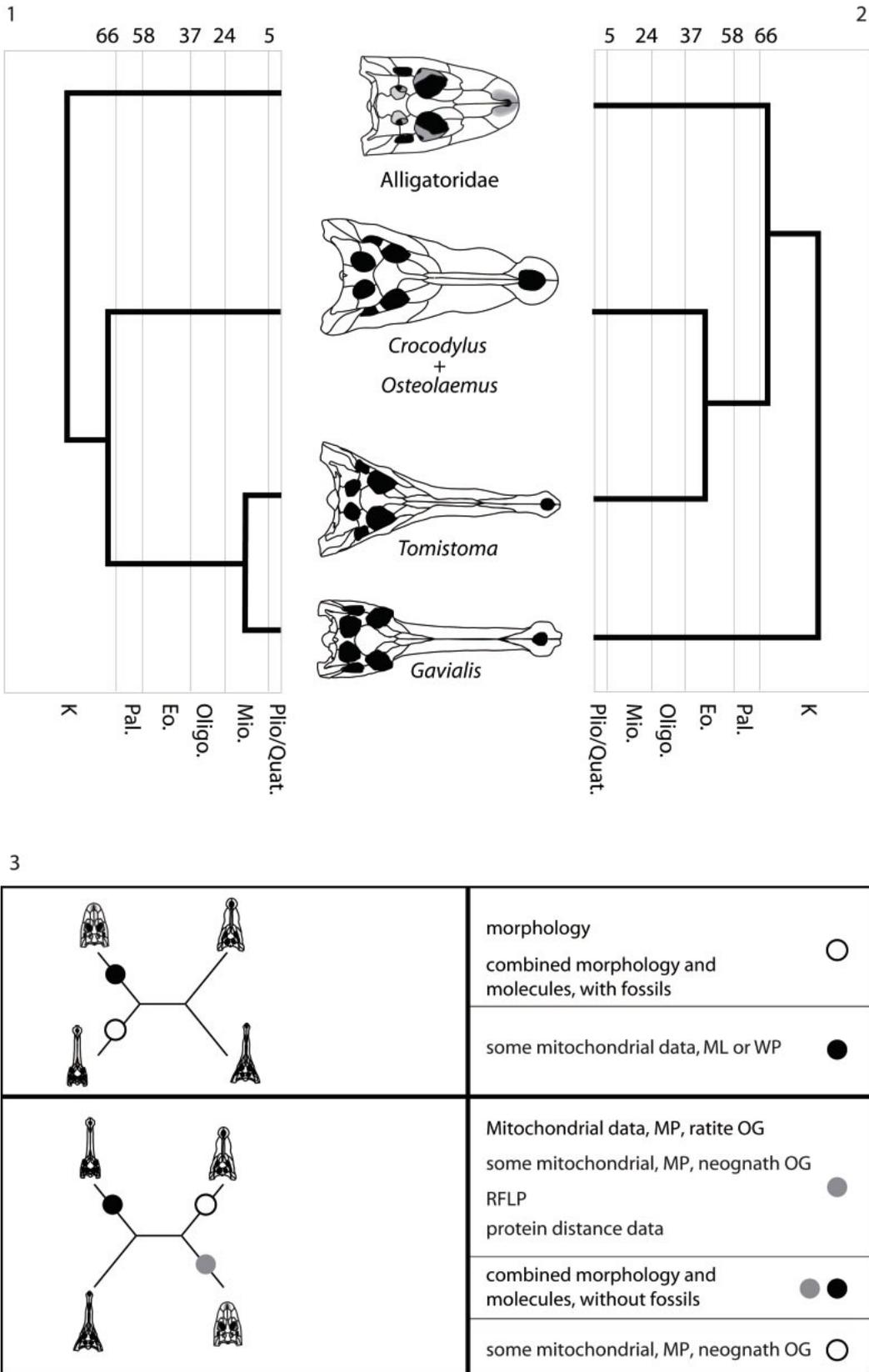


FIGURE 5—1, Relationships and divergence timing among extant crocodylians based on most molecular data sets. 2, Relationships and divergence timing based on morphology. 3, Underlying topologies and rootings for various data sets. Abbreviations: mp = maximum parsimony; ml = maximum likelihood; wp = weighted parsimony.

sets support this conclusion (Cracraft, 1988; Groth and Barrowclough, 1999; van Tuinen et al., 2000), but others do not (e.g., Härlid et al., 1998; Härlid and Arnason, 1999; Mindell et al., 1997, 1999). These latter studies are based on mitochondrial genes and ally the paleognaths with a clade including galliforms and anseriforms (Galloanserae), with Passeriformes (songbirds) forming the basalmost avian lineage (Fig. 4).

The role of taxon sampling in this disparity is debated (van Tuinen et al., 2000; Johnson, 2001). But strikingly, most non-mitochondrial analyses suggest that Galloanserae is the basalmost lineage within Neognathae. Because of the close relationship between Paleognathae and Galloanserae in mitochondrial analyses, one is tempted to suspect some sort of rooting issue. Groth and Barrowclough (1999) found that application of a more slowly-evolving gene supports a more conventional set of relationships, with Paleognathae and Galloanserae forming consecutive sister taxa to all other extant birds.

Divergence timing of extant bird clades.—At present, there are two general models for the diversification of avian lineages. One of these has been most explicitly developed by Feduccia (1995, 1996) and is based on an interpretation of the fossil record. Most Cretaceous neognath fossils are referable to predominantly aquatic or shore-dwelling groups (e.g., Olson, 1985, 1992; Olson and Parris, 1987; Noriega and Tambussi, 1995; Feduccia, 1996; Kurochkin, 2000). Some authors argue that all such fossils are either charadriiforms or “transitionals” between charadriiforms and other bird groups (Feduccia, 1995). The vast majority of neognath lineages first appear in the Eocene or later. A literal reading of this pattern leads to the conclusion that the ancestral neognath was shorebird-like, and that Neognathae experienced an explosive radiation following the Cretaceous-Tertiary extinction event, which claimed the lives of the widespread enantiornithine birds.

The second model is based primarily on molecular analyses of neognath relationships. Nucleotide sequence data uniformly indicates divergences among extant neognath “orders” within rather than after the Cretaceous (Hedges et al., 1996; Cooper and Penny, 1997; Waddell et al., 1999; van Tuinen and Hedges, 2001). This implies a large number of ghost lineages crossing the Cretaceous-Tertiary boundary and is partly congruent with earlier vicariance models of avian historical biogeography (Cracraft, 1974). A similar conflict is encountered with the divergence of mammalian “orders”—most first appear in the Tertiary, but molecular data suggest divergences in the Mesozoic (Bromham et al., 1999). If the primary divergences predated the Cretaceous-Tertiary boundary, one could conclude that the explosive radiation posited by the first model is an artifact of an incomplete fossil record and not a real phylogenetic pattern.

This conflict has been couched in “fossils versus molecules” rhetoric, and this is not altogether inappropriate—first appearances for crown-group birds are younger than 100 m.y. But in some ways, arguments against the fossil-based model are not arguing against a phylogenetic hypothesis as much as an ecological scenario. This is fundamentally different from the phylogenetic pattern used to derive molecular estimates. In a way, this is an apples-and-oranges comparison.

The conclusion that neognath groups sprang from a pool of shoredwelling ancestors is based on a literal reading of the fossil record and is not expressed as a hierarchical pattern. Regardless of the neognath phylogeny one chooses to accept, the presence of anseriforms and charadriiforms in the Late Cretaceous implies the presence of many other lineages at the same time (Cracraft, 2001). *Presbyornis*, a ducklike bird from the Lower Tertiary and, possibly, the Late Cretaceous (Olson, 1985; Noriega and Tambussi, 1995; Hope, 1998; Stidham, 1998b), was thought to represent a transitional form between basal shorebirds and anseriforms (Feduccia and Olson, 1980; Feduccia, 1994). But phylogenetic analyses clearly place *Presbyornis* within Anseriformes

and distant from charadriiforms (Livezey, 1997; Ericson, 1997; Stidham, 1998b). If anseriforms and galliforms are sister taxa, then discovery of a Cretaceous anseriform implies the presence of Galliformes in the Cretaceous, even if no such fossils have been found. Other interesting fossils, when considered in a phylogenetic framework, imply even more ghost lineages in the Cretaceous (Hope, 1998; Stidham, 1998a), though the identifications are not always accepted (Dyke and Mayr, 1999).

It thus seems that both sources of data support pre-Tertiary divergences among major avian lineages, provided both are examined in a phylogenetic light. One could even argue that both models are “correct,” in that the clades that diverged in the Cretaceous might have maintained low levels of diversity until after the Cretaceous-Tertiary boundary (Marshall, 1999; Cracraft, 2001; Fig. 6). The explosive-radiation model is an expression of diversification, not of divergence—we have more land birds in the Tertiary than in the Cretaceous, but this does not address the question of when these land bird groups diverged.

But we are still left with a significant gap between fossil first appearances in the Maastrichtian and molecular divergence estimates. Some molecular estimates put the neognath-paleognath and galloanserian-neavian splits prior to 100 m.y. and the division between oscine and suboscine passeriforms in the Cretaceous (Cooper and Penny, 1996; Kumar and Hedges, 1998; van Tuinen and Hedges, 2001). This implies that, for many avian clades, the known fossil range is much less than half of the group’s actual longevity (van Tuinen and Hedges, 2001).

The problem with this controversy is that the explanations put forth are largely ad hoc. We might as well assume that early avian clades were equipped with cloaking devices. Claims that the fossil record is simply incomplete make solid predictions of what should be discovered on the basis of a particular model, but do not directly address the problem at hand (Benton, 1999b). Arguments that fossil crown-group birds and mammals are known but not recognized because they lack diagnostic traits are also problematic. The fossils we have (and can identify) usually lack diagnostic traits for extant lineages and have diagnostic traits for extinct, unrelated lineages (Padian and Chiappe, 1998).

But conversely, claims that all modern bird clades experienced equivalent mutational speedups after the Cretaceous-Tertiary boundary, inflating genetic distances between species and causing molecular approaches to overestimate divergence timing, are also ad hoc. Most tests of rate heterogeneity cannot detect such phenomena. Those that can (e.g., Kumar and Hedges, 1998; Eastal, 1999) are based on other fossil-based calibrations that may be even more subject to biased sampling (for example, the bird-mammal split in the Carboniferous) than those being investigated.

Whatever the strengths of the different sources of data, they all have weaknesses. The fossil record for birds has exploded in recent years, but we are still working with extremely fragile skeletons; indeed, the fact that the record has expanded as much as it has should give pause to anyone believing the record to be well-sampled. That we usually cannot confidently identify fragmentary bird remains also implies the obverse—that we cannot rule out identity with one of the extant bird “orders.” Arguments that avian fossil sampling in the Cenozoic contradicts lineage extensions into the Mesozoic (Bleiweiss, 1998) assume Cenozoic levels of diversity within the clades being investigated (Marshall, 1999). Moreover, whatever arguments can be made about the randomness of fossil occurrence distributions over time, these occurrences are clearly not unbiased. As acknowledged by Benton (1999b), historical biogeographic studies suggest a Gondwanan (or even Antarctic) origin for bird “orders” (see also Cracraft, 2001). Benton (1999b) cited spectacular localities with breathtakingly preserved small animals—none of them members of extant avian “orders”—as evidence for sufficient sampling; but these localities

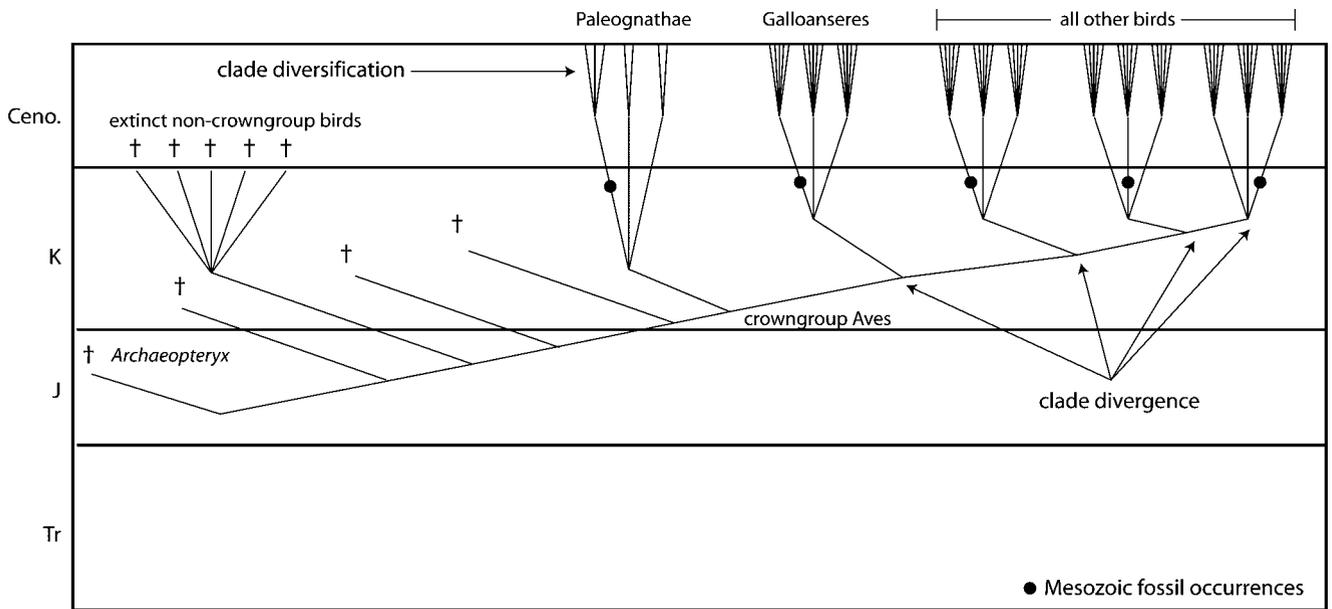


FIGURE 6—Distinction between divergence and diversification among birds. Lineage divergences can occur long before bursts of diversity; some argue that this explains the disparity between molecular and fossil temporal estimates within Aves.

are all Laurasian. The effect of *Lagerstätten* on avian stratigraphic ranges should not be understated—many clades first appear in the Eocene and Oligocene, but they more specifically tend to occur in places like the Green River Formation, the phosphorites of Quercy, or the Messel locality of Germany (Olson, 1985; Feduccia, 1996). And although the Late Cretaceous crown-group-free Malagasy site mentioned by Benton (1999b) shares faunal elements with other Gondwanan areas, it is also very endemic (Krause et al., 1999) and may not reflect vertebrate diversity elsewhere at that time.

Techniques for using molecular data to calibrate divergence times have grown more sophisticated, but they still suffer some limitations. A figure in Bromham et al. (1999, fig. 1) is particularly striking in this regard. Ranges of molecular divergence estimates increase markedly as we go back in time. Molecular clocks are less precise with older divergences. This is a familiar problem to paleontologists—absolute dating precision is usually coarser for older stratigraphic levels. Because the number of substitutions at a single site will increase with lineage age, we should expect older divergence estimates to be more dependent on the method used to generate them. And the quality of a molecular clock is still ultimately tied to the quality of the underlying fossil calibration.

SUMMARY

All of the remaining problems discussed in this paper involve, at some level, the relationships of lineages that are highly derived when they first appear in the fossil record. We find strong congruence among data sets when we sample basal fossils but run into problems when we do not. The earliest turtles and pterosaurs are derived enough to potentially erase telltale plesiomorphic features. The slender-snouted crocodyliforms that cause headaches are called “slender-snouted” for a reason, and our capacity to compile fossil ranges for extant bird lineages depends on our ability to recognize them in the first place.

I can envision no other solution than the continued effort to find fossils that will fill in the gaps, however long they are. And of course, we should continue to sample more genes for more

taxa, to refine our phylogeny reconstruction methods, and to investigate the ways in which molecules can calibrate divergences. Morphology and molecules are both heritable and must, at some level, reflect the same phylogenetic signal.

Archosaur systematists have reached remarkable consensus over most issues. Individual taxa may move here and there on the trees in Figures 1 through 4, but the gross relationships appear stable and will likely be reflected by most future discoveries. If this prediction proves incorrect, we will learn some exceedingly interesting things. We have seen one “golden age” of archosaur phylogenetics. The synthetic period we are entering, in which the kind of data used takes second stage to the question itself, will be another.

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