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12 Perspectives on Avian Origins

Lawrence M. Witmer

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ORIGINS OF THE HIGHER GROUPS OF TETRAPODS

Controversy and Consensus

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Before the work of John H. Ostrom in the 1970's, few contemporary scientists were interested in the origin of birds. Although the belief that birds were descended from reptiles was nearly universal, little research was directed toward developing a more specific hypothesis of avian ancestry. Most workers accepted the authoritative treatment of Heilmann (1927) that suggested that small early archosaurs ("pseudosuchian thecodonts") were involved in some way with the origin of birds. Ostrom's discovery and description of the small, birdlike theropod *Deinonychus* (Ostrom, 1969) ignited both the scientific community and the public. In the succeeding years, there has been an unrelenting flow of literature on dinosaurs and their physiology, the remarkable diversity of other archosaurs, and the origin of birds.

This and the following three chapters are devoted to this last topic. John Ostrom restates his well-known advocacy for the relationship of birds to coelurosaurian theropod dinosaurs and answers his critics. Samuel Tarsitano provides a novel approach to investigating avian ancestry and discusses features that suggest to him that birds descended from thecodonts. Larry Martin provides a detailed description of the Jurassic bird *Archaeopteryx* and reasserts the validity of his hypothesis that birds are closely related to crocodylians.

The present chapter summarizes the historical development of ideas on bird origins. Upon reaching the modern era (post-1970), I focus on the diversity of current opinion and attempt to put some of the recent contro-

versies in perspective. In all but a few cases, it is impossible to examine in detail the separate, but related, topic of the origin of avian flight (Padian, 1986). Although today we are in the period of liveliest discourse on the origin of flight, perhaps the most insightful historical review should await the passing of a few more years. Several papers have included short historical summaries of the debate on avian origins. Among the most important are those by Osborn (1900), Gregory (1916), Heilmann (1927), de Beer (1954), Ostrom (1976, 1985), Feduccia (1980), and Gauthier (1986). Furthermore, although his book is not dedicated to the subject, Desmond (1982) provided an engaging and well-researched account of the debate in mid-Victorian England. Rather than list all of the papers for or against a particular hypothesis (see de Beer, 1954, and Ostrom, 1976, 1985, for more comprehensive citations), I will examine some of the more important contributions in detail.

Three authors, more than anyone else, have shaped the debate on avian origins. T. H. Huxley (1868b, 1870a,b) developed the first well-articulated, specific argument for avian ancestry—the dinosaurian hypothesis. The second is Gerhard Heilmann (1927), whose monumental work *The Origin of Birds* held sway for 50 years. Its importance led Ostrom (1985:17) to exclaim rightly, “The impact of Heilmann’s book cannot be exaggerated. On the question of bird origins, its impact has been second only to the original discovery of *Archaeopteryx*.” The same easily can be said for Ostrom himself, whose series of papers (most elegantly, Ostrom, 1976) provided the focus for all later work.

There is a curious blending of the characters of the various reptilian groups in the Birds; there has been no exclusive adoption of the mode of structure of any one scaly type by these feathered vertebrates; those reptilian qualities and excellencies which are best and highest have become theirs; but how much more! This exaltation of the “Sauropsidan” or oviparous type by the substitution of feathers for scales, wings for paws, warm blood for cold, intelligence for stupidity, and what is lovely instead of loathsomeness,—this sudden glorification of the vertebrate form is one of the great wonders of Nature.

—William Kitchen Parker (1864:56–57)

AVIAN ORIGINS FROM LAMARCK TO 1970

Before evolutionary views were common, the origin of birds (or of anything else for that matter) was not an issue—all things were considered products of divine creation. Furthermore, the morphological gap between birds and other animals was so profound and the fossil record so poor that birds truly seemed to stand apart from the rest of the animal kingdom. The early pre-Darwinian evolutionists were limited to the

comparative anatomy of modern forms, a science that was still in its infancy. Lamarck (1809), for instance, derived birds from turtles, presumably on the basis of the rhamphotheca-covered, edentulous jaws; birds themselves (in particular, the penguins) then gave rise to the monstremes.

With the 1859 publication of Darwin's *On the Origin of Species*, evolutionary origins became an important issue, and, in fact, the origin of birds became a principal example of evolution (Evans, 1865; Huxley, 1868b). The discovery of the reptilian bird *Archaeopteryx lithographica* in the Jurassic limestones near Solnhofen, Bavaria, in 1861—less than two years after the publication of the *Origin*—would seem to have come at the best possible time for the Darwinians. But its intermediate characters were not missed by the antievolutionists. Andreas Wagner (1861, 1862:266) quickly wrote the first paper ever published on *Archaeopteryx* (Desmond, 1982) in hopes of “ward[ing] off Darwinian misinterpretations.” Wagner considered the fossil (which he named *Griphosaurus*) a feathered reptile of no special relationship to birds. Richard Owen (1862, 1863) described the London specimen and, rather than bemoaning its evolutionary implications, almost rejoiced in its support for his concept of the Archetype, noting that “we discern . . . a retention of a structure embryonal and transitory in the modern representatives of the class, and a closer adhesion to the general vertebrate type” (Owen, 1863:46).

Yet the evolutionary importance of *Archaeopteryx* eventually was seized upon—first by Evans (1865), who saw it as intermediate between birds and reptiles in general, and then Huxley (1868b), who used it in his discussion of the dinosaurian relationships of birds. In fact, Huxley's 1868 paper, his first on bird origins, was framed largely as a proof of evolution. Surprisingly, when Huxley (1868b:73) noted that “but a single specimen, obtained from those Solenhofen slates . . . affords a still nearer approximation to the ‘missing link’ between reptiles and birds,” he was referring not to *Archaeopteryx*, but to the small theropod *Compsognathus* (Fig. 1). He made no mention of any dinosaurian features of *Archaeopteryx* but used it simply as a demonstration of the existence of more reptilian birds. He made comparisons with large dinosaurs such as the ornithischians *Scelidosaurus* and *Iguanodon* and the carnosaur *Megalosaurus*, noting the large number of sacral vertebrae and the general birdlike nature of the pelvis and hind limb. However, the coup de grace of his argument was based on the birdlike characters of *Compsognathus* (viz., the generally gracile skeleton and very birdlike hind limb). Although we often regard Huxley as publishing on “avian origins,” Huxley's emphasis was more on placing dinosaurs (and *not* birds) within vertebrate phylogeny. The effect is the same; we read Huxley as stating that birds are related to dinosaurs, but he actually was arguing the converse.

Huxley's (1870a) “Further evidence” paper introduced a few additional

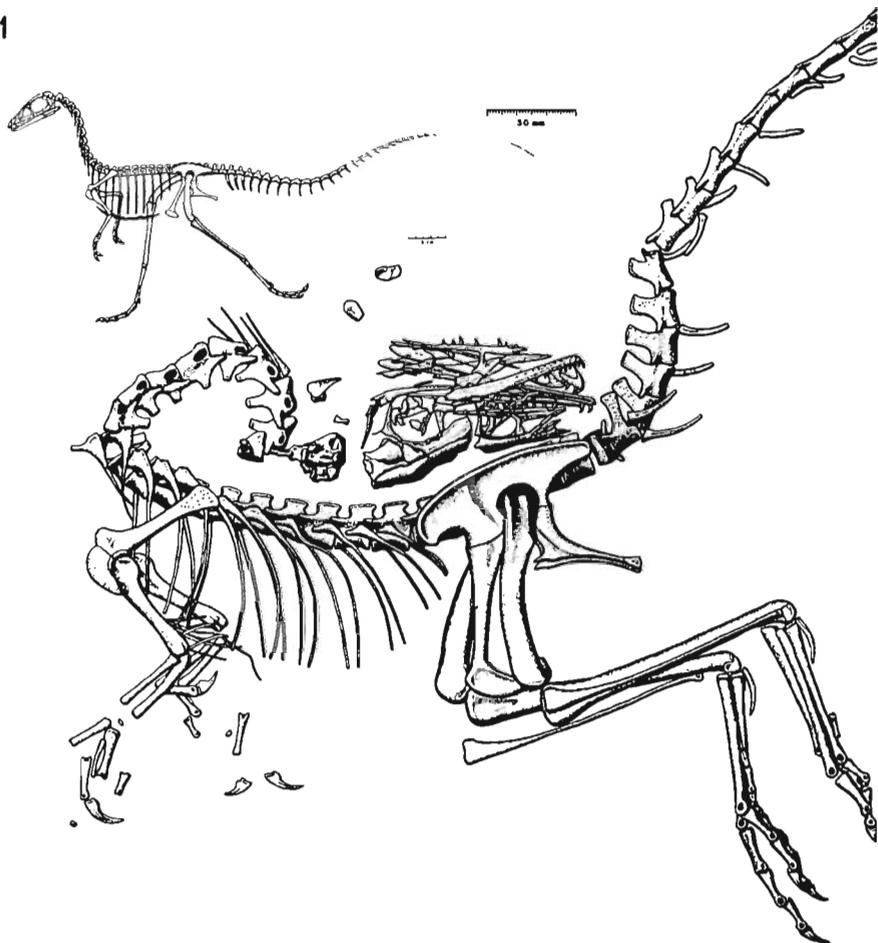


Fig. 1. Skeleton and restoration of *Compsognathus longipes*. (Modified from Ostrom, 1978, courtesy of Bayerischen Staatssammlung für Paläontologie und historische Geologie, Munich, Germany.)

characters supporting the dinosaurian relationships of birds such as tibial torsion and the ascending process of the astragalus. He also noted the similarities in the pelvis of birds and ornithischians such as *Iguanodon* and *Hypsilophodon*—that is, the elongate antacetabular ilium, the obturator process of the ischium, and the retroverted pubis. In fact, although impressed with the avian features of *Compsognathus* in the 1868b paper, he was also struck by the opisthopuby of *Hypsilophodon*, noting (1870a:28) that it “affords unequivocal evidences of a further step towards the bird.”

Later that year, Huxley published his classification of dinosaurs

(1870b). Within his Dinosauria were three families: Megalosauridae, Scelidosauridae, and Iguanodontidae. Excluding *Compsognathus* from Dinosauria, he made it "representative of a group equivalent to" Dinosauria. He united the two as Ornithoscelida. He asserted the "affinities" of Ornithoscelida with birds on the basis again of (p. 38) "the peculiarities of the hind limb and pelvis." He did not cite one "ornithoscelidan" that was closer to birds than another. Later, Haeckel (1907) adopted the taxon name and included *Compsognathus* and birds within his Ornithoscelides, a group that was itself subordinated to Dinosauria. Huxley did not consider such a specific position because he viewed the divergence of birds and dinosaurs as taking place in the Paleozoic. In fact, he considered *Archaeopteryx* almost irrelevant to the whole issue (Desmond, 1982), stating (Huxley, 1868a:248) "that, in many respects, *Archaeopteryx* is more remote from the boundary-line between birds and reptiles than some living *Ratitae* are." Huxley (1868b:75) "regarded as certain that we have no knowledge of the animals which linked reptiles and birds together historically and genetically, and that the *Dinosauria*, with *Compsognathus*, *Archaeopteryx*, and the struthious birds, only help us to form a reasonable conception of what these intermediate forms may have been." Later, however, Huxley (1882) vaguely proposed a more direct ancestry of birds (and crocodiles) from very early (perhaps hypothetical) dinosaurs.

Although Huxley deserves credit for his detailed analysis, actually he was preceded by two workers. Gegenbaur (1864) considered *Compsognathus* a phylogenetic intermediate between birds and reptiles on the basis of similarities in the tarsus. Cope (1867), in a brief note that appeared three months before Huxley's first bird-origin paper, considered birds to be related to both dinosaurs and pterosaurs. Penguins, or perhaps ratites, were closer to dinosaurs, and *Archaeopteryx* was closer to pterosaurs. Like Huxley, Cope also was struck by the avian features of *Compsognathus*. The points of resemblance between birds and dinosaurs included the crus, the astragalus, and "a more or less erect position" of the body (Cope, 1867). Whereas Gegenbaur and Cope did little subsequent work on the subject, Huxley's papers stimulated considerable research, and he is rightly credited for the dinosaurian hypothesis.

The controversy resulting from Huxley's papers centered on avian origins, as well as on evolution itself. It is surprising, therefore, that Charles Darwin made little of *Archaeopteryx* and the origin of birds. In later editions of *On the Origin of Species*, Darwin did not showcase *Archaeopteryx* as a long-sought evolutionary intermediate, but merely as a demonstration of "how little we as yet know of the former inhabitants of the world" (Darwin, 1872:315).

Support for Huxley's ideas came largely from outside England. Haeckel, of course, was the most vocal advocate in Germany for both

evolution and the reptilian relationships of birds. Whereas earlier, Haeckel (1866) placed birds close to turtles, pterosaurs, and “anomodonts” (a mixed bag composed of dicynodonts, prolacertids, and rhy-chosaurs), he later (Haeckel, 1875) included dinosaurs within this nexus (Fig. 2), citing Huxley’s comparisons of birds and *Compsognathus*. As mentioned, Gegenbaur (1864, 1878) made comparisons among birds, *Archaeopteryx*, and *Compsognathus* and, partly on the basis of the “tibio-tarsus” and long tail, united them in the subclass Saururi within the Sauropsida. Georg Baur (1883, 1884b, 1887) argued persuasively for the

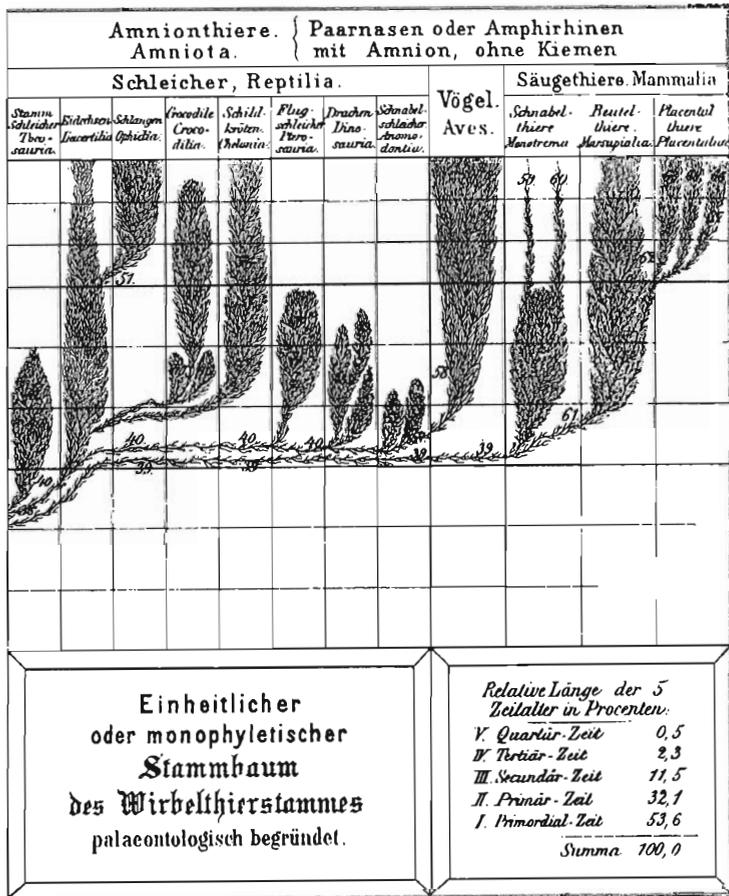


Fig. 2. Phylogeny of Amniota from Haeckel, 1875. The sister-group of birds is Anomodontia (“beaked reptiles”), which includes not only *Compsognathus* (which is not within Dinosauria) but also dicynodont therapsids. Successive out-groups are Dinosauria (“dragons”), Pterosauria (“flying reptiles”), and a group comprising squamates, crocodilians, and turtles.

dinosaurian origin of birds. In 1883, Baur made detailed comparisons of the ankles of birds and dinosaurs (and noted that the ontogeny of the avian tarsus recapitulates dinosaur phylogeny) but offered no specific hypothesis of ancestry within Dinosauria. However, his work on the pelvis (Baur, 1884b, 1887) led him to believe that, because of the presence of a “postpubis” in birds and ornithischians, it is “in the herbivorous Dinosaurs and especially in the ornithopod-like forms [that] we must seek for the ancestry of birds” (Baur, 1884b:1275). W. Dames (1884) took issue with Baur and others, and did not regard any of the resemblances in the pelvis and hind limb as indicative of phylogenetic relationship. Baur (1884a) answered Dames’s objections, and Dames (1885) published a bitter reply, criticizing Baur for his “unknown ancestor” of birds and for putting too much weight on too few characters.

In America, O. C. Marsh (1877) originally accepted that birds originated from *within* Dinosauria. However, he later adopted Huxley’s less specific hypothesis of common ancestry in the Paleozoic. In “Odontornithes,” Marsh (1880:188) reconstructed a hypothetical bird ancestor, “a form [that] would be on the road toward the Birds, rather than on the ancestral line of either Dinosaurs or Pterodactyles.” In 1881, Marsh reasserted the similarities of *Archaeopteryx* and *Compsognathus* but noted (p. 340) that “the two forms are in reality widely separated.”

In 1879, B. F. Mudge published a note objecting to the dinosaurian ancestry of birds. Mudge (1879:226) complained that only “a few species” of dinosaurs had avian characteristics and that “the dinosaurs vary so much from each other that it is difficult to give a single trait that runs through the whole. But no single genus, or set of genera, have many features in common with the birds, or a single persistent, typical element of structure which is found in both.” Mudge’s comments are justified if one accepts the then current notion of Huxley and Marsh that birds and dinosaurs share a common ancestry—in current parlance, if Aves and Dinosauria are sister-groups and if certain “avian” features are not also primitive for Dinosauria, then these features are indeed convergently evolved in those dinosaurs possessing them. In that same volume of the *Kansas City Review of Science*, S. W. Williston offered a rejoinder to Mudge in which, without fanfare, he suggested a much more specific view of the dinosaurian origin of birds. Williston (1879:458–459) acknowledged that “scarcely a single trait of structure runs through the whole of Dinosauria; but that fact does not affect the relation existing between the most avian dinosaurs and the most reptilian birds.” Williston was among the first to derive birds directly from a specific group of dinosaurs, noting that (p. 458) “true dinosaurs . . . may have given off branches that developed upwards into birds.” Thus, Williston answered Mudge by suggesting that avian features arose only once—in the dinosaurian clade of which

birds are a member. Although he did not name the dinosaurs close to birds, his description indicates Theropoda. Curiously, Williston (1925) later retreated from the specific position and presented a tree supporting Huxley's hypothesis of the common ancestry of birds and Dinosauria.

Huxley's great adversary Richard Owen (1875) offered a long criticism of Huxley's ideas on dinosaurs and birds. Owen viewed dinosaurs not as erect bipedal forms but as quadrupeds (some of which he regarded as aquatic). He examined some of the similarities between birds and dinosaurs cited in Huxley's papers and compared them with the stegosaur *Omosaurus* (= *Dacentrurus*, the main topic of the paper). It is no surprise that he found Huxley's similarities (as suggested by the more birdlike ornithopods and theropods) to break down when graviportal dinosaurs were considered. Interestingly, Owen (1875) never mentioned *Compsognathus*, Huxley's "missing link" between birds and dinosaurs. Instead, Owen cited resemblances of birds to mammals, in particular, monotremes. For example, according to Owen, some dinosaur-bird characters such as the opisthopuby noted by Huxley are found in only some dinosaurs but all mammals. Although earlier Owen (1870) had ascribed the similarities of birds and pterosaurs to convergence, he (1875:91) later considered pterosaurs to be the reptiles closest to birds but was ignorant as to "how the Rhamphorhynchus became transmuted into the Archeopteryx."

Because Huxley never responded to Owen's paper, Dollo (1883b:87) thought that it was "therefore quite necessary to fall in with the opinion of one or the other naturalist." The basis for most of Dollo's comparisons was the excellent *Iguanodon* material from Bernissart, Belgium. He made extensive comparisons with birds and found them to be remarkably similar (often "identical") in detail to *Iguanodon*. Although Dollo (1882, 1883a,b) often is cited as opposing the relationship of birds to dinosaurs (Osborn, 1900; Ostrom, 1976, 1985; Gauthier, 1986), Dollo's papers (especially 1883b) were directed primarily at proving *la station droite* (in effect, bipedality) in dinosaurs. In fact, he stated (Dollo, 1883b:88) that he "did not care for the present whether the points in common between dinosaurs and birds are coming from heredity or from adaptation." Nevertheless, Dollo (1883b) seems to have favored homology over analogy. He regarded Huxley's work as "classic" and arranged sauropods, ornithopods, and birds in a "phylogenetic series." Thus, rather than being an opponent, Dollo can be considered a supporter of dinosaurian relationships.

Owen was not the only worker to dissent from Huxley. Carl Vogt (1879, 1880) had rather peculiar and contradictory ideas about *Archaeopteryx* and the origin of birds; he was cited by de Beer (1954), Ostrom (1976, 1985), and Gauthier (1986) as supporting the derivation of birds from lizards.

Vogt (1880:452) identified few avian features in *Archaeopteryx* and considered it to be “a Reptile flying by means of feathers and perching with the legs of a Bird.” He rejected both Gegenbaur’s (1878) union of *Archaeopteryx* and *Compsognathus* into the Saururi and Huxley’s (1870b) common-ancestry hypothesis. Despite such stated views, Vogt (1880:454) suggested that “the Dinosaurs would lead to the Ratites, the *Archaeopteryx* to the Birds that fly.” He did not offer a specific group that led to the *Archaeopteryx*–volant bird line. Vogt (1880:456) “picture[d] . . . the ancestors of the *Archaeopteryx* as terrestrial Reptiles in the form of Lizards.” Contrary to the assertions of recent authors, Vogt did not suggest ancestry from Squamata, but only from a generalized reptile. However, Vogt’s major objection to the dinosaurian relationships of birds was one that has persisted to today; he considered any resemblances between dinosaurs and birds to be convergent and “only related to the development of the power of keeping an upright position upon the hind-feet” (Vogt, 1880:448).

Vogt’s idea of the separate origin of ratites and carinates from different nonavian stocks was not uncommon during this period. George Mivart (1881) noted only in passing his support for such a “double origin”—i.e., ratites from dinosaurs and carinates from pterosaurs. Robert Wiedersheim (1882, 1884, 1885, 1886), on the other hand, published several detailed accounts in which he argued for the diphyly of birds. Although de Beer (1954) and Ostrom (1985) viewed Wiedersheim as sometimes deriving *Archaeopteryx* from lizards (i.e., Squamata) and sometimes from pterosaurs, Wiedersheim’s actual position was stable and never involved relationships with Squamata (Fig. 3). According to Wiedersheim, pterosaurs and *Archaeopteryx* shared a common reptilian ancestor; the descendants of *Archaeopteryx* included *Ichthyornis* and all modern carinate birds. Wiedersheim envisioned a common dinosaurian ancestor shared by ratites and *Hesperornis*. These two great clades converge on an early Triassic or late Paleozoic common ancestor. Wiedersheim’s argument often is inconsistent internally, and it rested largely on the authority of others (e.g., Marsh’s [1880] assertion of ratite affinities for *Hesperornis*). Like Vogt, Wiedersheim was willing to accept large amounts of convergence.

H. G. Seeley was perhaps the first to argue for convergence. He stood up after Huxley read his “Further evidence” paper and “thought it possible that the peculiar structure of the hinder limbs of the Dinosauria was due to the functions they performed rather than to any actual affinity with birds” (in Discussion to Huxley, 1870a:31). Like Cope (1867) and Owen (1875), Seeley (1866, 1881) considered pterosaurs to be “allied” to birds (placing them as a subclass of birds in his 1866 paper) on the basis of elongate coracoids, keeled sterna, pneumatic limb bones, and other features; *Archaeopteryx* was a critical intermediate between pterosaurs and

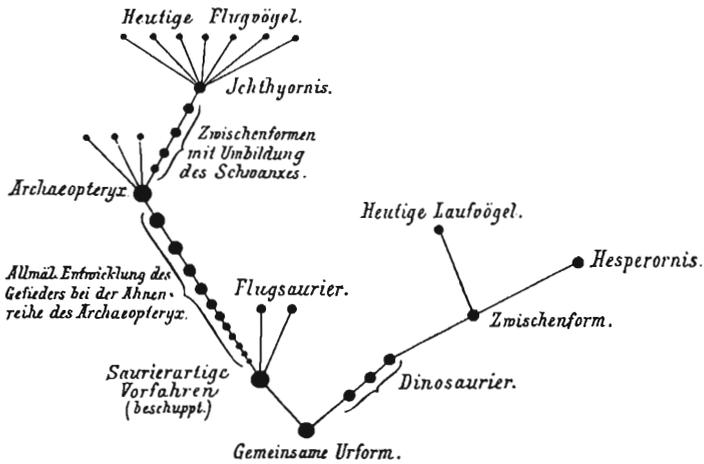


Fig. 3. Phylogeny of birds and their relatives from Wiedersheim, 1885. Living flying birds (*heutige Flugvögel*) are descendants of *Ichthyornis*. The line leading to *Archaeopteryx* shares a common "lizardlike ancestor" with pterosaurs (*Flugsaurier*). Ratites ("living running birds" or *heutige Laufvögel*) and *Hesperornis* represent a lineage descended from dinosaurs.

birds. Huxley (1870b:38) handled Seeley with a convergence argument of his own, stating that the similarities of pterosaurs to birds were the result of "physiological action, and not to affinity."

To summarize thus far, the theory of organic evolution opened the door for the discussion of avian origins. Although priority goes to Gegenbaur (1864) and Cope (1867), Huxley (1868b, 1870a) was the most visible proponent of the relationship of dinosaurs and birds. Huxley was joined by others such as Haeckel (1875), Marsh (1877), Williston (1879), Baur (1883), and Wiedersheim (1885). Many (Vogt, 1880; Seeley, 1881; Mudge, 1879; Dames, 1884; Parker, 1887; Fürbringer, 1888) discounted these resemblances, ascribing them to convergence. Others sought relationships with other groups, most often pterosaurs (Cope, 1867; Owen, 1875; Seeley, 1881; Mivart, 1881; Wiedersheim, 1885). Ostrom (1985:16) credited Fürbringer (1888) with "a compromise explanation—the common ancestor hypothesis." However, as elaborated above, the common-ancestor hypothesis was Huxley's from the beginning. In many respects, Huxley's views seem rather contradictory. He argued cogently for certain characters, such as the pelvis of ornithopods or the tarsus of theropods, as if they indicated monophyly of birds and a particular group of dinosaurs. But at the same time, he considered birds and dinosaurs to share a common ancestry in the Permian. Huxley never explicitly traced all his characters over all Dinosauria. Clearly, to postulate common ancestry of Aves and Dinosauria (i.e., a sister-group relationship) is to postulate convergence in many features of birds and higher dinosaurs.

H. F. Osborn (1900), who supported a “form of the Huxleyan hypothesis,” sought to reduce the impact of such convergence by arguing for the origin of birds from an early bipedal dinosaur. Osborn (1900:797), in effect, downgraded the convergence to parallelism by suggesting that “the numerous parallels and resemblances in dinosaur and bird structure, while quite independently evolved, could thus be traced back to a potentially similar inheritance.” This quotation articulates a common sentiment among workers in the late nineteenth and early twentieth centuries. Phylogenetic hypotheses often were vague, and people were willing to accept massive convergence. In fact, many workers (e.g., Lowe, 1935) followed Osborn in suggesting that convergence actually *demonstrated* some form of “affinity” as evidence of a shared genetic background.

Robert Broom (1906), on the other hand, suggested that the data should be accepted at face value and presented a phylogenetic tree to which some modern workers would not object: Aves is the sister-group of Theropoda, Pterosauria is the sister-group of these two, and a “*Proterosuchus*-like form” is the ancestor of these three. Broom rejected any notions of convergence in the hind limb, especially the tibia and tarsus—the resemblance is too good. Broom considered the avian-theropod “tibiotarsus” to have evolved in response to weight-bearing (exemplified in the larger theropods). On the other hand, he noted that the ancestor of flying birds must have been very small. Thus, although not explicitly stating it, Broom implied a process of miniaturization in the origin of birds.

The opening decades of this century witnessed a flurry of papers that focused mostly on the origin of flight and almost ignored the phylogenetic question. Pycraft (1906) was one among many to follow Marsh’s (1880) scenario for the arboreal origin of avian flight and was the first to reconstruct a hypothetical “Pro-Aves.” Pycraft considered the ancestor of birds to be a quadrupedal lizardlike reptile that leaped and parachuted from tree to tree. Similar views were espoused by C. W. Beebe, who in 1915 proposed an arboreal “Tetrapteryx stage in the ancestry of birds” in which feathers projected from both forelimbs and hind limbs, the latter forming a “pelvic wing.” As with many authors of this period, Beebe’s views on the precise phylogenetic position of birds were unclear, and he regarded “the ancestral stems of alligators, *Dinosaurs*, and birds [as] gradually approaching each other until somewhere, at some time, they were united in a common stock” (Beebe, 1906:8).

Franz Nopsca (1907:234) dissented from these views (see Weishampel and Reif, 1984, for further analysis) and, like Williston (1879), argued instead for a terrestrial origin of flight “*from bipedal long-tailed cursorial reptiles which during running oared along in the air by flapping their free anterior extremities*” (italics in original). Nopsca found no similarities between

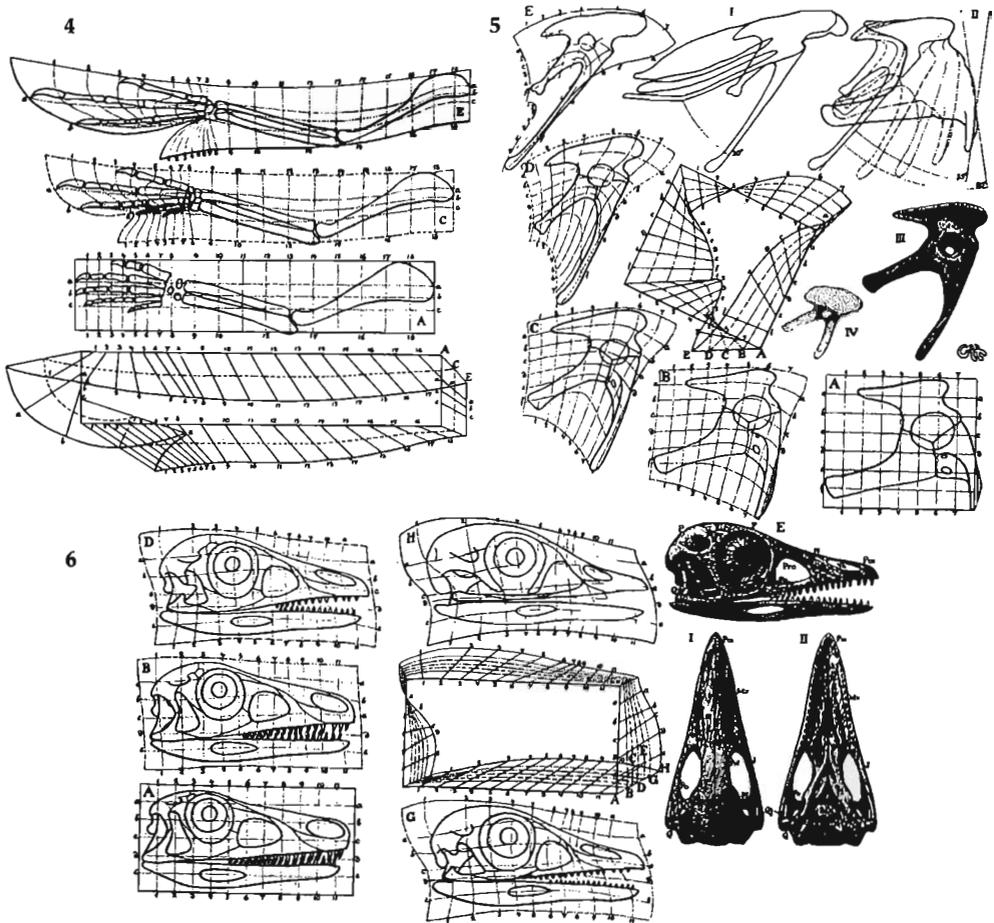
birds and arboreal mammals such as squirrels and primates but noted great similarity between birds and the obviously ground-dwelling dinosaurs. Nopsca (1923) refuted the evidence of Pycraft, Beebe, and others who argued for an arboreal proavis and reasserted the resemblances of birds and especially theropod dinosaurs. Contrary to Pycraft (1906), Nopsca (1907, 1923) regarded the avian and dinosaurian "cannon bone" clearly as a terrestrial adaptation and cited resemblances with hopping animals like dipodid rodents. However, Nopsca never offered a specific hypothesis of avian relationships; birds were descendants of "Dinosaur-like Reptiles." In his 1929 paper, Nopsca, like Huxley and Osborn, suggested a common ancestry of birds and dinosaurs in the Permian; he agreed with Osborn (1900), without citing him, that the common ancestor presumably resembled something like the prolacertiform *Proterosaurus*.

Nopsca's unwavering support for the cursorial origin of birds and flight was not fully accepted by his contemporaries. Othenio Abel (1911) agreed that birds and theropods possessed important similarities and was among those who argued for a common ancestry. For Abel, however, this common ancestor was an arboreal animal. The avian descendants of this ancestor simply remained in the trees, whereas the theropods became secondarily terrestrial. Some workers sought a compromise and considered the ancestors of birds to be scansorial or partly arboreal. O. P. Hay (1910:22–23), for example, suggested that the proaves were "accustomed to clamber[ing] about over rocks and shrubs and the limbs of trees . . . running or making leaps to catch their prey or to escape capture by their enemies." Hay considered birds to be descended from dinosaurs and even identified the specific group that served as avian ancestors. He regarded ornithischians as being derived from theropods, and sauropods as being an older group. Because, Hay surmised, birds arose earlier than the theropod-ornithischian line, "the sauropods are nearest the stock from which sprang the birds, and it is in their skeletons that we must seek for the primitive common characters" (Hay, 1910:23). W. K. Gregory (1916) also believed that the ancestors of birds were both arboreal and terrestrial but lamented (p. 37) that "the immediate ancestry of the birds is regrettably indecisive." Gregory favored origin of birds from somewhere within the nexus of early dinosaurs and the recently discovered pseudosuchians.

In fact, the description of the Triassic "pseudosuchian thecodont" *Euparkeria* by Robert Broom in 1913 had such an impact that *Euparkeria* deserves to join *Archaeopteryx* and *Deinonychus* as among the most influential fossil evidence in the debate on avian origins. Broom (1913) included within his Pseudosuchia a number of early archosaurs in addition to *Euparkeria*, such as *Ornithosuchus* and *Scleromochlus*. Broom considered the

Pseudosuchia to either “have affinities with” or be ancestral to Theropoda, Pterosauria, and birds. He (with many later workers) regarded these early archosaurs as being simply “primitive enough” to be ancestral to the later forms. Furthermore, the pseudosuchian origin of birds helped answer objections that dinosaurs or pterosaurs were too specialized to serve as avian ancestors. Broom considered this perfectly consonant with his 1906 paper in which he argued “that the bird had come from a group immediately ancestral to the Theropodous Dinosaurs” and the “Pseudosuchia . . . proves to be just such a group” (Broom, 1913:631). Thus, Broom’s concept of the pseudosuchian origin of birds is really just a more specific version of Huxley’s common ancestry hypothesis. Broom’s (1913) characterization of Pseudosuchia marks an important shift of emphasis in the debate away from dinosaurs. The shift often was subtle. For example, if two of Abel’s works—one before (1911) and one after (1920) Broom’s 1913 paper—are examined closely, one notes that Abel’s position had *not* changed substantially; birds and theropod dinosaurs share a common ancestor. But in the later work, the tone of the comparisons with dinosaurs has softened. Whereas earlier, Abel (1911) wrote about the “homology” of bird and theropod hands, he later (1920:389) said that “the hand structure [of theropods] greatly *reminds one*” (italics added) of birds.

Broom’s treatment of pseudosuchians had a strong influence on Gerhard Heilmann’s discussion of avian ancestry in the 1927 classic *The Origin of Birds*. Apparently it is not well known that Heilmann published a series of long papers (e.g., Heilmann, 1916) in Danish on the same subject. These papers include the major features of the 1927 book and a number of figures and analyses that were omitted from the book (most notably, Cartesian transformations of the skull, limbs, and pelvis of pseudosuchians into those of his proavis; Figs. 4–6). Abel (1920) drew heavily from Heilmann’s (1916) paper. Nevertheless, Heilmann’s book in English (1927) is rightly credited with restructuring the debate. Heilmann was well versed in the anatomy and embryology of modern amniotes, and much of the book is spent with documenting (p. 138) “with absolute certainty . . . that the birds have descended from the reptiles” and have no close phylogenetic relationship with mammals. He also was familiar with the morphology of the important fossil taxa, and Part IV, entitled “The Proavian,” is devoted to determining which group is closest to birds. Heilmann assessed pterosaurs, ornithischians, coelurosaurs, and pseudosuchians, in turn, and finally reconstructed in detail his version of the hypothetical proavis. He found that the similarities between birds and pterosaurs generally were superficial. Furthermore, he stated (p. 141) that “the shoulder-girdle [of pterosaurs] has no clavicle, and so the birds cannot possibly descend from these reptiles.” This quotation illustrates a guiding principle of Heilmann’s book—i.e., Dollo’s law of



Figs. 4-6. D'Arcy Thompson grids (Cartesian transformations) depicting changes occurring in the evolution of birds from primitive archosaurs (from Heilmann, 1916). (4) Transformations in the forelimb of *Ornithosuchus* (A), Heilmann's hypothetical proavis (C), and *Archaeopteryx* (E). (5) Transformation in the pelvis of *Euparkeria* (A), intermediate forms (B-D), and *Archaeopteryx* (E); I depicts changes occurring from *Archaeopteryx* to *Hesperornis*; II depicts changes occurring from *Euparkeria* to *Archaeopteryx*; III is the hypothetical proavis; and IV is an embryonic gull. (6) Transformation in the skull of a generalized early archosaur (A), intermediates (B-D), Heilmann's proavis (E, I-II), a hypothetical early bird (G), and a schematic modern bird (H).

the irreversibility of evolution: that which is lost cannot be regained. Before beginning his analysis of the fossil groups, Heilmann asserted (p. 140) that "when strictly adhering to this law, we shall find that only a single reptile-group can lay claim to being the bird-ancestor."

Heilmann (1927) was not at all impressed with any of the similarities between birds and ornithischian dinosaurs—certainly none of the sim-

ilarities that are not also found in small theropods. Because the ornithischian pelvis previously had received so much attention in the discussion of bird origins, Heilmann analyzed it in detail. He remarked (p. 148) that "the mere fact that [the pubis] was directed backward, like that of the birds, has evidently so hypnotized several scientists that they have overlooked, or tried to set aside, the many conspicuous differences between the birds and the Predentates [Ornithischia]." Heilmann considered the ornithischian prepubic process of the pubis to be homologous to the pubis of other animals and the postpubic process to be a neomorph, but modern interpretation suggests the reverse.

Numerous workers have noted that Heilmann (1927) cited a large number of detailed similarities throughout the skeletons of birds and small theropods such as *Procompsognathus*, *Compsognathus*, *Ornitholestes*, and ornithomimids. For instance, with respect to the "metatarsals and toes," he remarked that "the resemblance is so close that we should take them to be two species within the same genus, and not the representatives of two different classes" (Heilmann, 1927:176). From his analyses he concluded that (p. 183) "it would seem a rather obvious conclusion that it is amongst the Coelurosaurs that we are to look for the bird-ancestor." However, because "the clavicles are wanting" in coelurosaurs, his unflinching adherence to Dollo's law forced him to accept that "these saurians could not possibly be the ancestors of the birds" (p. 183). Nevertheless, Heilmann suggested that the ancestor of birds was "closely akin to the Coelurosaurs" but "wholly without the shortcomings" (p. 185). Thus, although many modern workers have interpreted Heilmann (1927) as rejecting any relationship with theropods, he actually argued for something closer to the common-ancestry hypothesis of earlier workers such as Broom (1913).

Like Broom (1913), Heilmann (1927) regarded pseudosuchian thecodonts as the group without these "shortcomings." Heilmann reiterated his adherence to Dollo's law and emphasized the *presence* of clavicles in these primitive archosaurs. He also discussed the great similarity between the skulls of pseudosuchians such as *Euparkeria*, *Aetosaurus*, and *Archaeopteryx*. It should be noted, however, that his reconstruction of the Berlin *Archaeopteryx* (Fig. 7C) seems to be based largely on imagination. (The Berlin skull is poorly preserved.) Moreover, the details bear a suspicious resemblance to *Euparkeria* and *Aetosaurus*, which would make any phylogenetic inferences rather circular.

Heilmann (1927) cited other resemblances of pseudosuchians and birds. For instance, the pubis "excites our interest" because it is twisted and "looks as if it were about turning backwards, thus exactly fulfilling our expectations as to the pubis of a bird-ancestor" (p. 189). Reasserting his belief in the closeness of small theropods to avian ancestry, he envi-

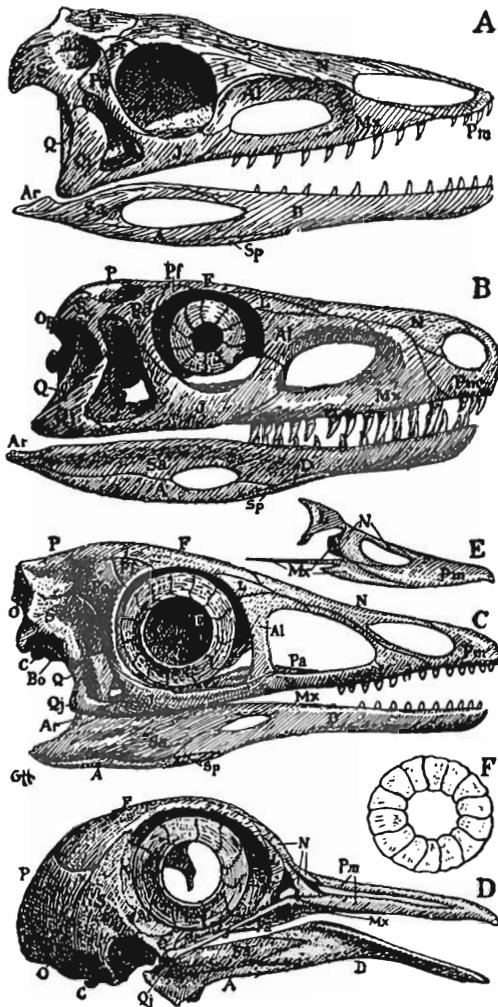


Fig. 7. Perhaps the most reproduced and redrawn figure from Heilmann's (1927) *Origin of Birds* (reprinted courtesy of Dover Publications). (A) Triassic archosaur, *Aetosaurus ferratus*. (B) Triassic archosaur, *Euparkeria capensis*. (C) *Archaeopteryx lithographica*, based on the Berlin specimen. (D) recent pigeon, *Columba livia*. (E) upper jaw of a juvenile duck, *Aythya ferina*. (F) sclerotic ring of a thalattosaur, *Thalattosaurus alexandrae*.

sioned (p. 189) the forelimb of pseudosuchians "passing [through] transitional stages, probably resembling the corresponding forms in the Coelurosaur." Although Heilmann was forced to reject theropod ancestry because of Dollo's law, he (p. 191) accepted pseudosuchians as avian ancestors simply because "nothing in their structure militates against the view that one of them might have been the ancestor of the birds." He regarded the origin of birds to have proceeded first through a terrestrial, cursorial stage in which the hind limb evolved its avian characteristics (fusion and elongation of metatarsals, and the like) and then an arboreal, climbing stage in which the flight-related forelimb characters appeared.

Interestingly, Heilmann agreed with Abel (1911) that some theropods (e.g., the ancestor of *Ornitholestes* and ornithomimids) also went through an arboreal stage that produced their rather avian tridactyl hands.

Heilmann's (1927) *Origin of Birds* was written authoritatively, well illustrated, and well referenced. Rather than stimulating research on avian origins, it nearly halted further study. The pseudosuchian ancestry of birds (and of virtually all later archosaur groups) became dogma and found its way into the popular literature as well as scientific texts. For example, Heilmann's (1927) figures and restorations (such as Fig. 7) must rank among the most reproduced drawings in the history of paleontological illustration. The pseudosuchian hypothesis was (and remains) a nonspecific hypothesis—birds came from pseudosuchians, but precisely which pseudosuchians is unknown.

Although there was broad acceptance of the pseudosuchian hypothesis, it was not universal. Nopsca (1929), for example, published a response to Heilmann's book reasserting the origin of birds from "dinosaur-like" forms and, more vigorously, the cursorial origin of avian flight. He was strongly opposed to the arboreal proavis and reiterated the cursorial features of birds. There was no "clavicle problem" for Nopsca, because he regarded the avian furcula as a neomorphic ossification; thus, there was no violation of Dollo's law.

J. E. V. Boas (1930) also disagreed with the conclusions of Heilmann (whom he regarded as an "amateur ornithologist") and proposed an interesting alternative. He did not even acknowledge the pseudosuchian hypothesis but reproduced some of Heilmann's figures. Boas's analysis comprised the pelvis of birds and ornithischians and the manus and pes of birds and small theropods. With respect to the similarities in the pelvis, he considered it "unthinkable that such a completely congruous and complex specialization should have taken place twice in the course of phylogenetic history" (Boas, 1930:224). Later, however, after discussing the hands and feet, he remarked (p. 244) that "birds are derived from forms that are quite closely related to compsognathids [in which he included *Compsognathus*, *Ornitholestes*, and ornithomimids], perhaps even were members of this family." Boas resolved this conflict by noting that some ornithischians, such as ceratopsians, lost the postpubic process of the pubis, resulting in a saurischian-like pelvis. He suggested that this was also the case for his "compsognathids" which, by implication, became derived ornithischians. Thus, the ancestor of birds had an ornithischian pelvis and the extremities of a small theropod. Boas's hypothesis seems to have attracted little support from his contemporaries.

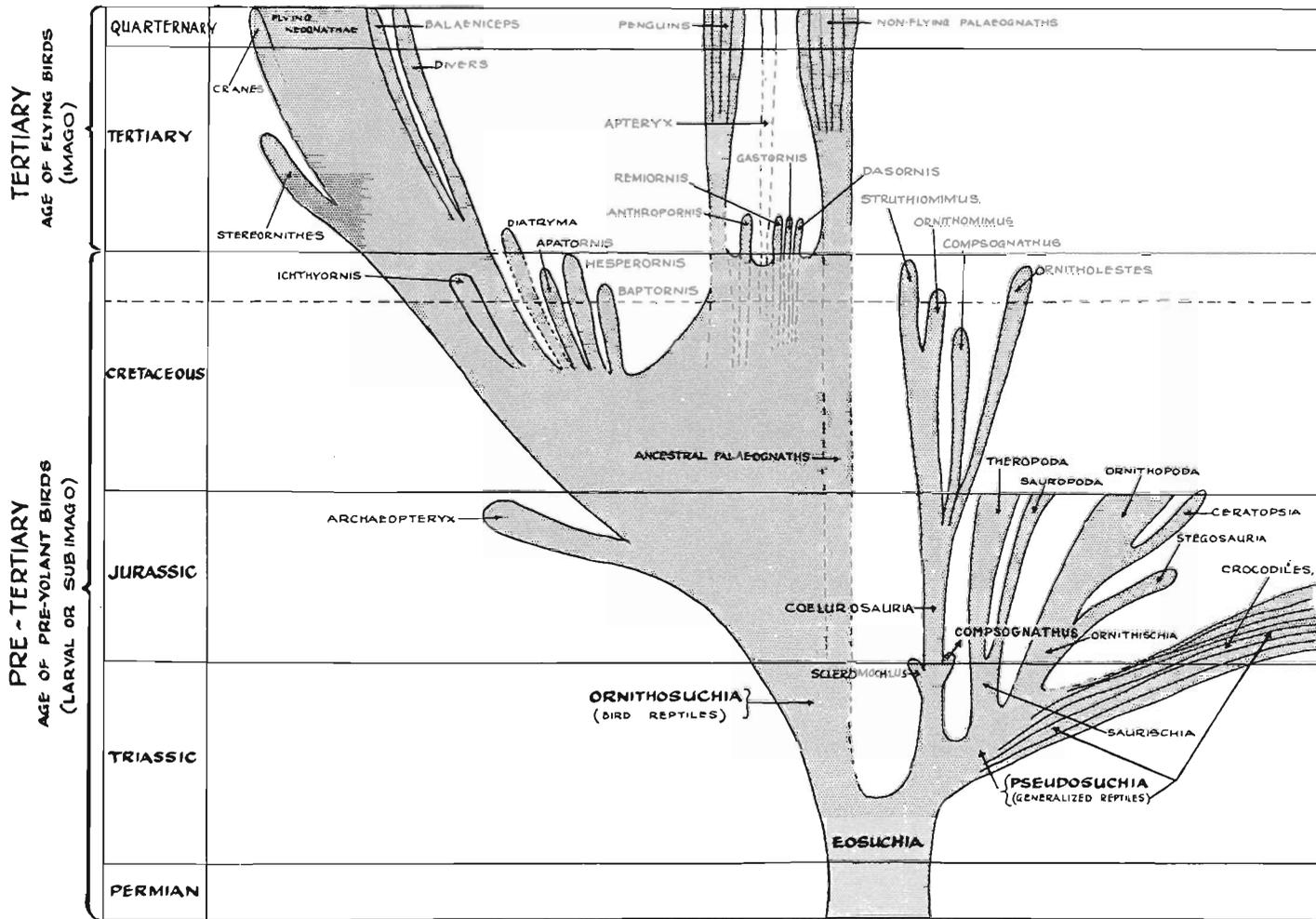
Branislav Petronievics published a series of papers (mostly in the 1920's and summarized in Petronievics, 1950) on the morphology of *Archaeopteryx*. He considered the ancestor of birds to be among a "primitive group

of lacertilians," but he never made detailed comparisons of birds and squamates or formulated any cogent arguments on avian ancestry. Like many others, Petronievics attributed all similarities between birds, pterosaurs, and dinosaurs to convergence.

Whereas the ideas of Boas and Petronievics seem to be little more than "aberrations" in the post-Heilmann period, those of Percy Roycroft Lowe stimulated an intense debate. Lowe was cited widely as being among the few in the period between Heilmann and Ostrom to argue for the dinosaurian relationships of birds. Lowe's ideas, however, are complex, often contradictory, and were not offered as explicit statements on avian origins. Lowe was interested principally in ratites, and all his comments on avian origins stem from his views on the relationships of ratites to reptiles and other birds. His main thesis, first stated in 1928, was that ratites are *not* secondarily flightless birds that evolved from volant birds via degeneration, but rather that they represent an ancient group that branched off from the avian clade before the evolution of flight. In 1928, Lowe cited Broom and Heilmann and considered (p. 210) ratites to be "direct line relics of an ancient avifauna which marked an early stage in the evolution of the bird from some Proto-Pseudosuchian ancestor." His comparisons of ratites with theropods were not intended to suggest monophyly of the two groups but only analogous patterns of morphological evolution. For example, the reduction of the forelimb in ratites culminating in kiwis is analogous to the same reduction seen in theropods, which culminated in the tyrannosaur condition.

Lowe's 1935 paper is cited most often as indicating his views on the monophyly of birds and dinosaurs. However, he reiterated (p. 400) his belief "in fixing upon the Eosuchia [early diapsids] as, at any rate, forming a provisional ancestral base from which sprang both dinosaurian reptiles and birds" (Fig. 8). Thus, similar features arose independently in birds and dinosaurs, not as a result of similar adaptation, but instead, because there "were resident potential genetic factors" in their eosuchian ancestor which allowed avian or reptilian characters "to crop up almost indiscriminately in any descendent branch" (Lowe, 1935:402). A necessary corollary to Lowe's ratite hypothesis was that *Archaeopteryx* was a flying dinosaur and not a bird at all. He was willing to accept (p. 409) "the diphyletic origin of feathers—a zoological transgression for which I expect no mercy." Lowe (1944) expanded on the dinosaurian nature of *Archaeopteryx* and predicted the discovery of feathers on *Ornitholestes*.

Fig. 8. Phylogeny of birds and most other archosaurs from Lowe, 1935 ("On the relationship of the Struthionies to the dinosaurs and to the rest of the avian class," *Ibis*, courtesy of Blackwell Scientific Publications). Ratites are close to coelurosaurs on the diagram, but their common ancestor lived in the early Triassic and is neither a bird nor a dinosaur.



Hypothetical Scheme to show relations of the Bipedal Dinosaur to the Struthionae

The 1944 paper is contradictory with regard to avian origins. At times, Lowe advocated the parallel evolution hypothesis of his earlier papers, but once (p. 522), he suggested a direct ancestor-descendant relationship. When examining Lowe's concept of avian origins, one must remember that his main focus was on ratites. Whereas earlier he had advocated the then-favored pseudosuchian hypothesis, the logical extension of his views on ratites forced him to accept several controversial propositions (e.g., *Archaeopteryx* was not a bird; feathers evolved twice). In summary, it clearly is inappropriate simply to list Lowe with those advocating the origin of birds from theropod dinosaurs—it is both inaccurate and obscures the interesting and idiosyncratic nature of his arguments.

Lowe's conclusions were neither ignored nor accepted. Gregory (1935) and Tucker (1938) offered rebuttals to Lowe, but they were concerned more with ratites than with avian origins. Simpson (1946) also responded to Lowe, asserting views that were to become dogma. According to Simpson, any similarities of birds and theropods are convergent. *Archaeopteryx* was a bird. Flight originated in the trees, and birds evolved from generalized pseudosuchian thecodonts. De Beer (1954, 1956) also refuted the arguments of Lowe, reasoning that *Archaeopteryx* is intermediate between reptiles and higher birds, and that ratites had ancestors that flew.

Lowe's ideas were not universally rejected, however. Nils Holmgren's work on avian phylogeny, published posthumously in 1955, supported some of Lowe's conclusions. For instance, Holmgren (1955) considered the ancestor of ratites to have been flightless. Whereas Lowe (usually) regarded theropods and birds as having taken parallel evolutionary courses, Holmgren posited a direct ancestor-descendant relationship. He answered Heilmann's (1927) complaint of the absence of clavicles in theropods by suggesting that they may have been present and (p. 306) "were either cartilaginous, membranous or merely present as rudiments in embryos." If this were the case, then clavicles were obtained owing to "reappearance or rejuvenation in the birds, after a long period of apparent absence in the Coelurosaurs" (p. 322). Whereas Lowe postulated the diphyletic origin of feathers, Holmgren suggested a monophyletic origin, proposing (p. 307) "that the ancestors of the birds were down-clad reptiles, belonging to a reptile stem issuing from Coelurosaurs." "[In fact] when comparing the hand of *Ornitholestes* with that of *Archaeornis* [= *Archaeopteryx*] it is difficult to avoid the thought that it was the developing wing feathers that caused the lengthening of the fingers in *Ornitholestes* and that in the Coelurosaurs there were the makings of an avian wing" (Holmgren, 1955:309). Regarding flight, Holmgren considered the "proavis" to be divisible into two parts—a cursorial "pro-ratite" and an arboreal "pro-carinate." Both proaves were coelurosaurs, but the procarinate had better developed feathers.

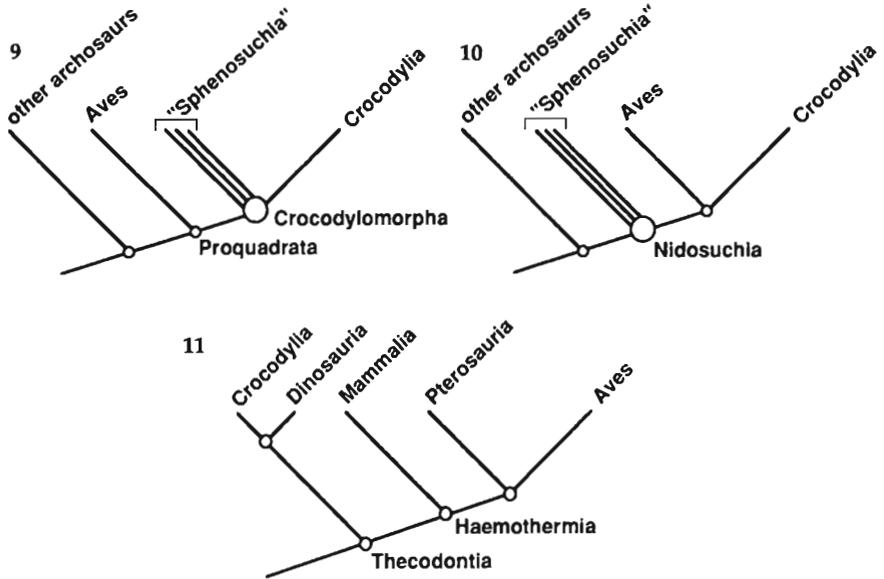
Holmgren's (1955) work generated virtually no controversy; it was almost as though the paper never had appeared. All the reviews that immediately followed (e.g., de Beer, 1956; Swinton, 1958, 1960; Romer, 1966; Bock, 1969; Brodkorb, 1971) do little more regarding avian origins than recite Heilmann's conclusions about *Euparkeria*, *Ornithosuchus*, and the pseudosuchian origin of birds. None of these authors even cites, let alone refutes, Holmgren (1955). The pseudosuchian origin of birds was the unquestioned dogma heading into the 1970's. As Bock (1969:148) noted, "acceptance of [pseudosuchians as avian ancestors] is more by default than by direct demonstration."

AVIAN ORIGINS FROM 1970 TO THE PRESENT

Beginning in the 1970's and continuing to the present, there has been renewed interest in the *specific* position of birds within vertebrate phylogeny. Primary reasons for this recent attention include the discovery of new birdlike archosaurs and a much closer examination of details of archosaur anatomy. Furthermore, the growing popularity of Hennigian systematic methodology (cladistics) has shifted the focus to obtaining more specific hypotheses of relationships and has introduced new organisms and new characters to the debate. As this is relatively recent history and most of these views are well known, I do not examine these efforts in as much detail but focus on the diversity of opinion.

Peter Galton (1970) initiated this period of activity by resurrecting the hypothesis that had been advocated earlier by Baur (1884b, 1887) and Boas (1930)—viz., the ornithischian relationships of birds. Galton's argument rested almost completely on the shared possession of a retroverted pubis and did not cite or discuss the other resemblances noted by Huxley, Baur, or Boas. He regarded ornithischians as being too specialized to serve as the ancestral stock and postulated a mid-Triassic common ancestor that was a cursorial, opisthopubic, bipedal dinosaur with none of the other ornithischian characters. Galton's formulation of the hypothesis was no more successful than Baur's or Boas's in attracting support. In fact, he later abandoned the hypothesis in favor of Ostrom's theropod-bird hypothesis (Bakker and Galton, 1974).

A new view on avian origins appeared when Alick Walker (1972, 1974) suggested that crocodylomorphs and birds constitute a monophyletic group (Fig. 9). Much of his evidence was based on the Triassic "sphenosuchian" *Sphenosuchus*, which he viewed as intermediate in many respects between birds and crocodylians. His evidence included aspects of cranial pneumaticity, cranial kinesis, palatal structure, inner-ear morphology, and the articulations of the quadrate. Walker (1977:320) suggested that the common ancestor of birds and crocodylomorphs was at "a



Figs. 9–11. Phylogenetic relationships of birds and various other Amniota based on the analyses of (9) Walker (1972, 1977); (10) Whetstone and Whybrow (1983) and Martin (1983a,b); taxon names are from Whetstone and Whybrow (1983); and (11) Gardiner (1982). In (9) and (10), “Sphenosuchia” is shown as paraphyletic on the basis of the analysis of Benton and Clark (1988).

higher level of organization than that of the Thecodontia” and erected “a new Class, the Proquadrata, to include the Sphenosuchia, Crocodylia and Aves as subclasses.”

Support for a sister-group relationship of birds and crocodylians came from K. N. Whetstone and L. D. Martin (1979, 1981), who accepted Walker’s (1972) characterization of the braincase articulations of the quadrate. They further proposed that the presence of a fenestra pseudorotundum (a release window associated with the recessus scala tympani) and tympanic pneumaticity represented synapomorphies of birds and crocodylians. Martin et al. (1980) offered another character complex as evidence of crocodylian relationships—i.e., tooth morphology and replacement. The evidence can be summarized as four synapomorphic character complexes: (1) a bipartite articulation of quadrate to braincase, (2) the fenestra pseudorotundum, (3) tympanic pneumaticity, and (4) dental features (Martin, 1983a,b, this volume; Whetstone, 1983; Whetstone and Whybrow, 1983).

Although it is usually referred to as the “crocodylian hypothesis,” the position of Walker, Martin, and Whetstone more properly should be called the “crocodylomorph hypothesis,” because all crocodylomorphs

(i.e., "sphenosuchians" and Crocodylia) are under consideration. These three workers accepted the monophyly of Sphenosuchia, but the recent analysis of Benton and Clark (1988) showed this assemblage to be paraphyletic. Close examination shows that Martin (1983a,b) and Whetstone and Whybrow (1983) proposed a somewhat different hypothesis than did Walker (1972, 1977). Walker considered birds to be the sister-group of crocodylomorphs as a whole (Fig. 9). Martin and Whetstone, on the other hand, regarded birds as the sister-group of crocodylians, with "sphenosuchians" being the sister-group of these two (Fig. 10). Thus, given a cladistic classification, Martin and Whetstone implied that birds are crocodylomorphs.

Walker's (1972) formulation did not initiate an immediate response. Ostrom's (1973) ideas on the coelurosaurian origin of birds, appearing less than a year after Walker's (1972) paper, were not presented as a refutation of Walker but rather as supporting an alternate hypothesis. In fact, most workers (e.g., Bakker and Galton, 1974; Thulborn, 1975) considered Ostrom's analysis so compelling that they dismissed the evidence for crocodylomorph relationships without comment.

It was only after Martin and his students made their contributions that the crocodylomorph hypothesis was evaluated critically. Tarsitano and Hecht (1980) critically examined the crocodylomorph hypothesis and stated objections that have been echoed by many later workers (e.g., Thulborn and Hamley, 1982; Hecht, 1985). They summarized Walker's data and correctly concluded that many of Walker's characters are either primitive or spurious. Tarsitano and Hecht (1980) rejected Whetstone and Martin's (1979) character of the fenestra pseudorotundum but did not discuss the pneumatic characters. McGowan and Baker (1981) questioned the pneumatic synapomorphies because air spaces are found in the skulls of theropods such as *Troodon* (= *Saurornithoides*). Molnar (1985) and Currie (1985) reported cranial pneumaticity in other theropods and also suggested that such evidence diminishes the crocodylomorph hypothesis. Indeed, the presence of cranial air sacs seems to be almost universal in archosaurs (Witmer, 1987). Crocodylomorphs, some theropods, birds, and even pterosaurs possess certain pneumatic features. Clearly, there has been much homoplasy. Early claims (e.g., Whetstone and Martin, 1981; Whetstone and Whybrow, 1983; Witmer, 1984) that possession of tympanic pneumaticity in birds and crocodylomorphs represents strong evidence for monophyly were premature. Archosaurian cranial pneumaticity is only beginning to be understood (Witmer, 1990), and the homology of many sinuses has yet to be demonstrated. Until these homologies are determined, one should remain cautious about any phylogenetic conclusions.

Padian (1982) and Gauthier and Padian (1985) also rejected the croco-

dylomorph hypothesis, but more on the grounds of parsimony than on the evidence. Put simply, the hypothesis that birds are theropods is better corroborated; thus, any similarities of birds and crocodylomorphs are deduced to be convergences. Gauthier (1986) evaluated the characters offered in support of the crocodylomorph hypothesis and presented the first significant challenge to the dental characters proposed by Martin et al. (1980) and Martin (1983a,b), noting that the absence of these apomorphies in otherwise derived crocodylomorphs suggests that birds and crocodylians acquired the dental features independently.

Perhaps the biggest blow for the crocodylomorph hypothesis came when Walker, the founder of the hypothesis, announced that "the original concept of a particularly close relationship between birds and crocodiles has become so tenuous that it is very difficult to sustain" (Walker, 1985:133). Further study of *Sphenosuchus* and the aetosaur *Stagonolepis* led Walker (1985) to believe that birds and crocodylians had acquired their apomorphic quadrate-braincase articulations independently and in different ways. Because the position of the quadrate head greatly constrains otic morphology, Walker reasoned that the other otic apomorphies also may have arisen convergently. The recognition that the skull of *Sphenosuchus* was not kinetic may have led Walker to recant, because cranial kinesis was such an important part of his earlier argument. Although other advocates of the crocodylomorph hypothesis (e.g., Martin, 1983a,b) always had regarded *Sphenosuchus* as akinetic and agreed with much of the criticism leveled at Walker, the rhetorical value of the abandonment of an idea by its initial proponent is seldom missed in a hot debate, and this is no exception (see, e.g., McGowan, 1985; Gauthier, 1986; Paul, 1988b; Gauthier and Padian, 1989).

Nevertheless, the crocodylomorph hypothesis still is regarded as tenable by Martin (this volume) and, in a modified form, seems to have attracted the support of Tarsitano (1985b, this volume). Although Tarsitano maintained that the immediate ancestor of birds was a thecodont, it seems that he now views that avian ancestor as also being close to crocodylomorphs. Tarsitano (1985b, this volume) did not necessarily exclude theropods from the crocodylomorph-bird clade and suggested that the presence of a vertical basicranium and a basisphenoid sinus in carnosaurs and crocodylians "may indicate their common ancestry in the early Triassic or Upper Permian" (Tarsitano, 1985b:40). Tarsitano (this volume) reiterates his conviction that birds, crocodylomorphs, theropods, and at least some thecodonts (specifically *Postosuchus*) may constitute a monophyletic group, with Aves apparently being the most primitive taxon (because birds plesiomorphically retain a flat basicranium). Unfortunately, Tarsitano has not discussed explicitly the evolution of his characters throughout archosaurs, and it is unclear if he accepts the monophyly of Pseudosuchia, Theropoda, Saurischia, or Dinosauria.

In many respects, the crocodylomorph hypothesis can be considered a specific version of the pseudosuchian thecodont hypothesis. As mentioned, Tarsitano and Hecht (1980) discussed and rejected both theropod and crocodylomorph relationships and offered a "new version" of Heilmann's pseudosuchian hypothesis. They partitioned thecodonts on the basis of the possession of armor and ankle type, and they concluded that birds originated from unarmored mesotarsal thecodonts, a group that also was ancestral to dinosaurs. Their cladogram placed the origin of birds somewhere between *Euparkeria* and *Lagosuchus* (a derived mesotarsal form). They were not explicit as to which taxa are included in their Pseudosuchia and which pseudosuchian was closest to birds. The new pseudosuchian hypothesis is similar to Heilmann's (1927) in that it centers on forms that are deemed "primitive enough," offers no synapomorphies of birds and known thecodonts, and ascribes all resemblances with theropods to homoplasy. It differs in that it predicts that some crocodylomorph apomorphies will be found in the pseudosuchian ancestor of birds.

In support of the pseudosuchian hypothesis, Tarsitano (1985a, this volume) has presented a novel solution to the problem of avian ancestry. Put simply: use aerodynamic principles to determine the most likely model for the origin of flight, create a hypothetical proavis, and then search Archosauria for a match. Hecht and Tarsitano (1982), Martin (1983b), Hecht (1985), Tarsitano (1985a, this volume) viewed the ancestor of birds as small, arboreal, and quadrupedal, as their model for the arboreal origin of flight dictates. Tarsitano (1985a, this volume) therefore has rejected the theropod hypothesis because known theropods, being too large and demonstrably terrestrial, fail the tests predicted by the arboreal theory. Instead, all of these authors point to small Triassic forms such as *Cosesaurus*, *Longisquama*, and *Megalanacosaurus* as being the sort of animals they envision in the arboreal model and that may be close to avian ancestry. Unfortunately, these taxa are poorly known, and some may not even be archosaurs. *Cosesaurus* recently was reclassified as a prolacertiform (Sanz and Lopez-Martinez, 1984). Another problem is the assumption that theoretical analysis of the origin of flight will answer the phylogenetic question. If a cursorial, terrestrial aerodynamic model were accepted, would these authors deny that a "thecodont" could be the terrestrial cursor and then throw their support to the theropod hypothesis? Conversely, what about arboreal theropods? Abel (1911) viewed theropods as originating in the trees. More recently, Paul (1988b) advocated both an arboreal origin of flight and a theropod origin of birds; he even illustrated a feathered *Ornitholestes* clambering about the branches.

Criticism of the pseudosuchian hypothesis came from supporters of theropod relationships. Ostrom (1976) was faced with the Heilmann version of the pseudosuchian hypothesis, which had been dogma for

decades. Ostrom found that pseudosuchians indeed were “primitive enough” to be avian ancestors but that no pseudosuchians displayed any unique avian apomorphies. Furthermore, Ostrom noted that the absence of clavicles in theropods (which had forced Heilmann [1927] to accept the pseudosuchian over the theropod hypothesis) was more apparent than real, in that several theropod specimens were preserved with clavicles. Thulborn and Hamley (1982), responding to the Tarsitano and Hecht (1980) version, criticized the latter for their “process-of-elimination” approach and lack of synapomorphies; they discounted the sole synapomorphy of *Archaeopteryx* and *Euparkeria* postulated by Tarsitano and Hecht (1980). Thulborn and Hamley (1982) denied that the new version was more informative than Heilmann’s version, noting that *Euparkeria* is among the most primitive and *Lagosuchus* among the most derived thecodonts and that suggesting that birds originated somewhere between the two is not saying much.

Perhaps the sharpest criticism came from Gauthier and Padian (1985, 1989) and Gauthier (1986), who argued that because Thecodontia is a paraphyletic taxon (and thus has the same diagnosis as Archosauria), it is meaningless to state that birds arose from them; such a statement implies only that birds are archosaurs. Although strictly true in a cladistic sense, saying that birds arose from a thecodont states not only that birds are archosaurs but also that they are *not* pterosaurs, crocodylomorphs, or dinosaurs. I agree with Gauthier and Padian, however, that a paraphyletic grade comprising early archosaurs (i.e., Thecodontia) should be abandoned, especially as our knowledge of the diversity and relationships of archosaurs improves. Gauthier and Padian (1985) also disapproved of the traditional composition of Pseudosuchia, which included most of the early archosaurs. Pseudosuchia indeed has become a “taxonomic wastebasket.” They provided a new composition, resulting in a monophyletic Pseudosuchia. Unfortunately, this new combination excludes some traditional “pseudosuchians,” such as *Euparkeria* and *Ornithosuchus* and, more importantly, includes Crocodylia, which are “true” suchians (= crocodile). It would be better to abandon the name Pseudosuchia altogether, or at least restrict it to meanings closer to its original usage, as advocated by Benton and Clark (1988). Similarly, we should abandon the “pseudosuchian hypothesis” of avian origins. That birds arose from unknown early archosaurs remains a valid hypothesis that could be falsified by demonstration of relationships with a known group; however, it is uninformative and does not suggest specific areas of research.

Perhaps the most surprising development in the debate on the origin of birds came when Brian Gardiner (1982) denied that birds were archosaurs and gave a cladistic justification for Owen’s Haemothermia (= Mammalia + Aves) (Fig. 11). Most of Gardiner’s data came from soft

anatomy, although he did consider a few fossil groups. Pterosaurs were placed as the sister-group of birds. Dinosaurs were united with crocodiles as Archosauria. Archosauria was the sister-group of Haemothermia. Løvtrup (1985) offered his support and contributed a few additional characters. Aside from Janvier (1983), few workers have cited Gardiner, let alone evaluated his data. Gauthier (1986) praised Gardiner for his cladistic methodology but faulted him for his grasp of the morphology and literature. Gauthier et al. (1988) provided a convincing refutation of Gardiner (1982), demonstrating that a consideration of all the evidence (both soft and hard parts) and all the taxa (both living and fossil) embeds birds firmly within a more traditionally construed Archosauria.

Whereas only a handful of recent workers have favored mammals, crocodylomorphs, or “thecodonts” as the sister-group or ancestors of birds, the majority of researchers believe that birds are closely related to theropod dinosaurs. The importance of John Ostrom’s efforts in shaping the current debate on avian origins cannot be overstated. In 1973, he laid out the basic plan of his argument in a one-page paper in *Nature*, which he then followed with a series of papers on the origin of birds and of avian flight. Ostrom’s 1976 paper in the *Biological Journal of the Linnean Society* rightly can be considered a landmark effort. Ostrom’s basic hypothesis is that birds are descended from a specific subset of Theropoda—small coelurosaurian theropod dinosaurs similar to *Ornitholestes* and *Deinonychus*. Ostrom’s comparisons almost always made reference to *Archaeopteryx* rather than to recent birds. Ostrom’s evidence came principally from the postcranium. (Interestingly, virtually all of the characters of the crocodylomorph hypothesis are cranial.) Although Ostrom found derived similarities throughout the skeleton, the following characters are perhaps the most important to the debate—(1) the phalangeal formula and proportions, and the pattern of digital reduction in the manus; (2) a semilunate carpal; (3) elongation of the forelimb and especially the manus; (4) a rodlike pubis with a distally expanded “foot”; (5) an ascending process of the astragalus; (6) a mesotarsal ankle joint; (7) the reduction of Metatarsal V and the loss of the connection between Metatarsal I and the tarsus; and (8) a reversed hallux. In a related series of papers (e.g., Ostrom, 1974, 1979, 1986) Ostrom championed the “cursorial predator” theory of the origin of avian flight, arguing that the morphology of *Archaeopteryx* is that of a terrestrial cursor and that Solnhofen paleoecology indicates an absence of trees or nearby cliffs from which gliding could take place.

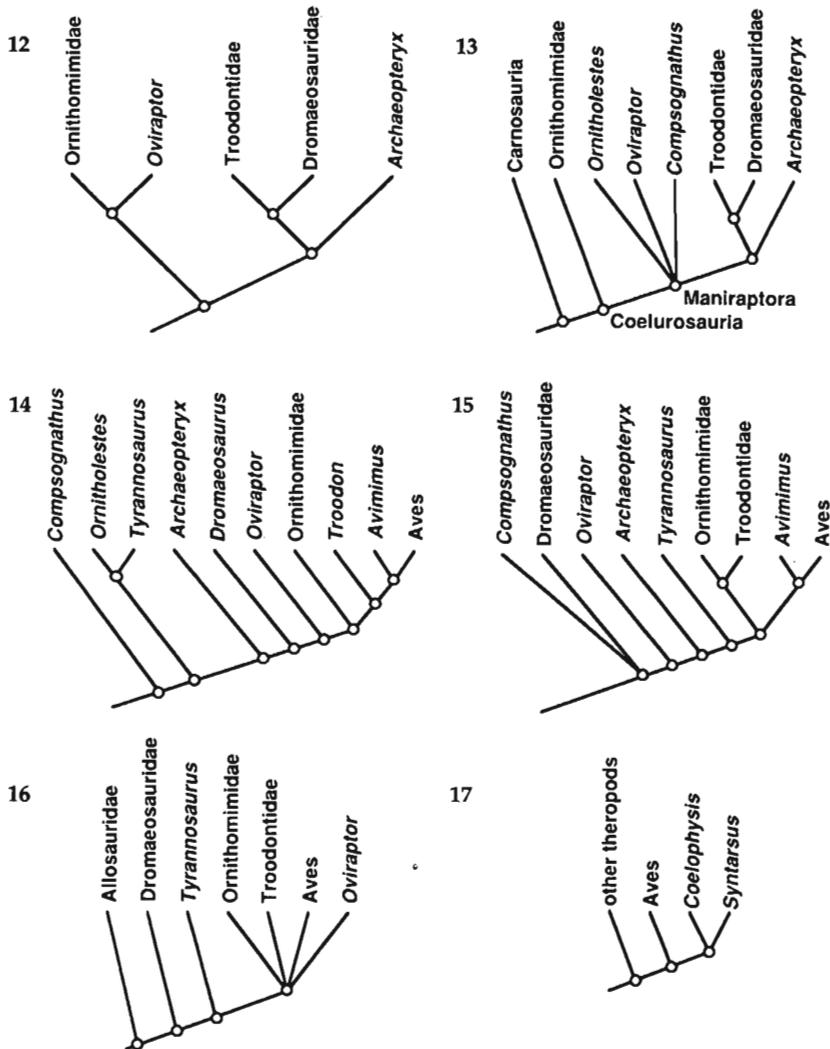
Ostrom’s coelurosaurian hypothesis was accepted almost immediately. Bakker and Galton (1974), Bakker (1975), and Thulborn (1975), among others, seized upon Ostrom’s findings, often using the hypothesis as the basis for radical new taxonomies or broad physiological inferences.

Although “not trying to create a bandwagon over Ostrom’s papers,” Cracraft (1977:492) applauded Ostrom for a “masterful job” and “meticulous work.” The initial response was not entirely positive, however, and Hecht (1976) claimed that many of Ostrom’s characters were of “low weight” or, reminiscent of the nineteenth-century responses to Huxley’s ideas, convergences resulting from shared bipedal habits.

Tarsitano, Hecht, and Martin have been the most vocal opponents of the theropod hypothesis and have leveled attacks at several of the important characters employed by Ostrom. Tarsitano and Hecht (1980) and Hecht and Tarsitano (1982) offered a series of arguments in refutation of theropod relationships. They regarded the manual digital homologies of birds and theropods to be different. They ascribed the similarities in the manual phalangeal formula and the presence of an ascending process of the astragalus in *Archaeopteryx* to preservational artifact, but both of these claims have been disproved (Wellnhofer, 1985, and Martin, this volume, respectively). Resemblances in the wrist were viewed as nonhomologous, and much similarity in the shoulder girdle and pubis was denied. Finally, they dismissed the reflexed hallux as a synapomorphy because it is absent in known theropods. Martin et al. (1980) and Martin (1983a) also attacked the character of the ascending process of the astragalus, stating that whereas theropods indeed possess such a process, birds have a separate neomorphic ossification, the pretibial bone. Martin (1983a,b, this volume) has joined Tarsitano and Hecht in questioning the homology of the semilunate carpal.

Although Ostrom (1976) did not present a cladogram, he stated that he tried to use only shared-derived characters when drawing phylogenetic conclusions from his data. Ostrom, however, never named a specific sister-group of birds. Although he noted more similarities between *Archaeopteryx* and dromaeosaurids such as *Deinonychus*, Ostrom (1976:173) concluded that birds descended from “a small unknown *Ornitholestes*-like coelurosaurian dinosaur.” Padian (1982:390) provided the first true cladogram of *Archaeopteryx* and other archosaurs in hopes “that the ambiguities of Ostrom’s approach can be remedied by more rigorous phylogenetic analysis.” In Padian’s scheme (Fig. 12), *Archaeopteryx* is the sister-group of deinonychosaur (Troodontidae + Dromaeosauridae). Although admittedly preliminary and incomplete owing to space restrictions, Padian’s (1982) analysis lacks much character analysis and does not include all the relevant taxa. This was rectified in large measure by Gauthier and Padian (1985), who provided cladograms and diagnoses of the archosaurian higher taxa and of saurischian taxa (again with birds as the sister-group of deinonychosaur). Gauthier (1986) reviewed the data supporting Ostrom’s hypothesis and provided detailed character analysis within a phylogenetic framework.

Padian (1982, 1985) and Gauthier and Padian (1985) based their model



Figs. 12–17. Phylogenetic relationships of birds and various other theropod dinosaurs on the basis of the analyses of (12) Padian (1982), (13) Gauthier (1986), (14) Paul (1988b), (15) Thulborn (1984), (16) Bakker et al. (1988), and (17) Raath (1985). In most cases, these authors included other taxa in their cladograms; I have included only the genera or major higher taxa discussed in the text.

for the origin of avian flight on their phylogenetic conclusions. Like Ostrom, they accepted the possibility of an arboreal origin but favored the cursorial predator hypothesis because the ancestors of birds were terrestrial, obligate bipeds that used their elongate forelimbs in prey manipulation. In fact, they argued that *Archaeopteryx* exhibits no forelimb

modifications beyond those seen in deinonychosaurs and that the latter already had the basic down-and-forward forelimb motion that became perfected into the avian flight stroke. They recognized that the arboreal theory may be more intuitively satisfying but argued (as did Ostrom) that their model better accounts for the data and makes fewer appeals to hypothetical intermediates. See Martin (this volume) and Tarsitano (this volume) for views counter to this functional interpretation.

Although Ostrom unquestionably deserves most of the credit for the wide acceptance of the theropod hypothesis, the importance of Gauthier's extensive phylogenetic analysis also must be recognized; it is more than just a formalization of Ostrom's data. As mentioned, Padian (1982) and Gauthier and Padian (1985) published cladograms that embedded birds firmly within Theropoda; Padian's (1982) analysis employed 49 synapomorphies, whereas Gauthier and Padian (1985) reported more than 120. However, Gauthier's 1986 revision of the Saurischia (including birds) is the first paper that provides adequate character analysis (84 characters), the inclusion of many (17) taxa, and a character-taxon matrix. He also justified the broader phylogenetic context of his analysis by including diagnoses and discussions of other archosaurian taxa. Rather than discuss all the characters, I review a few of the more important aspects of Gauthier's (1986) analysis (Fig. 13). Whereas Ostrom built his hypothesis primarily on postcranial characters, Gauthier added 13 cranial synapomorphies (e.g., subsidiary antorbital fenestrae, antorbital tooth row), although a few are not present in birds because they are so specialized. Sixteen characters come from the vertebral column and an additional 14 from the hand and wrist.

As birds are regarded as derived coelurosaurs, Gauthier (1986) focused on relationships within Coelurosauria and not Ceratosauria or Carnosauria (Fig. 13). Unfortunately, he was not able to clarify relationships very much, principally because so many of the taxa are poorly known. Coelurosauria is composed of Ornithomimidae and an unresolved polytomy named Maniraptora. Among maniraptorans, birds and deinonychosaurs are sister-taxa. A problem is that deinonychosaurs may not be monophyletic. Gauthier (1986) united troodontids and dromaeosaurids into the Deinonychosauria on the basis of the shared possession of a raptorial second digit of the foot. Currie (1985), however, presented evidence supporting monophyly of troodontids and ornithomimids on the basis of derived cranial characters also shared with birds. Thulborn (1984) and Bakker et al. (1988) also concluded that troodontids and ornithomimids form a clade independent of dromaeosaurids (Figs. 15–16). Furthermore, Paul (1984, 1988b) and Bakker et al. (1988) argued that troodontids are related more closely to birds than are dromaeosaurids (Fig. 14). Gauthier (1986:47) acknowledged that there is "doubt on the

monophyly of Deinonychosauria." The question arises that if troodontids are indeed related to ornithomimids and birds form a clade with troodontids, then what becomes of relationships within Coelurosauria? Another matter complicating Gauthier's (1986) analysis is that he did not consider the peculiar Mongolian theropod *Avimimus*—a form so birdlike that Thulborn (1984) and Paul (1988b) regarded it as the sister-taxon of birds (Figs. 15, 14), and Molnar and Archer (1984) went so far as to include *Avimimus* within Aves. (Molnar [1985] retreated from this extreme position.)

Despite these problems, Gauthier's (1986) analysis is still the benchmark to which subsequent studies should refer until it is supplanted by a new, even better corroborated hypothesis. Although polyphyly of the Deinonychosauria may be possible, it awaits demonstration by phylogenetic analysis of all relevant taxa. Those who disagree with Gauthier's conclusions must (1) discredit Gauthier's entire analysis by demonstrating *numerous* mistakes in character analysis, and (2) propose a similarly explicit phylogenetic hypothesis incorporating all pertinent taxa and accounting for Gauthier's characters. It is insufficient to dismiss the entire analysis by showing problems in a few characters or by proposing that a single "complex" character indicates different relationships. Likewise, as numerous authors have pointed out, convergence cannot be invoked in an ad hoc manner but must be deduced from the topology of the cladogram. At present, supporters of relationships of birds with either crocodylomorphs, "thecodonts," or mammals have failed to produce a competing cladogram, and in this respect the coelurosaurian hypothesis is uncontested. Gardiner (1982) came the closest, but Gauthier et al. (1988) successfully refuted mammalian relationships with the twofold approach advocated above.

Tarsitano (this volume) attempts the first approach by seeking to discount Gauthier's (1986) character analysis of the Maniraptora. Tarsitano performs the tedious (but necessary) character-by-character evaluation and objects that many of Gauthier's characters could be described and illustrated better, a criticism also raised by Martin (1988). Many of Tarsitano's points involve arguments of convergence, and he dismisses many characters because they are found in pterosaurs or turtles or mammals. Clearly, these comparisons are irrelevant. Even ornithischians are too distantly related to be useful in character polarization of maniraptorans. Furthermore, he rejects several characters because in these cases convergence was "easy" or "necessary" for biomechanical reasons. Thus, in these cases, Tarsitano demonstrates only that convergence is *possible*, not that it occurred.

Although Ostrom, Padian, and Gauthier argued that birds are related most closely to deinonychosaurian coelurosaurs, theirs is not the only

hypothesis on the theropod relationships of birds. Ostrom (1976) and Padian (1985) regarded *Archaeopteryx* as being the necessary focus of any discussion of avian origins. This view is not universally held, however. Several workers recently have suggested that *Archaeopteryx* was a feathered coelurosaur that had little to do with the immediate ancestry of birds. As early as 1975, Thulborn (p. 268) referred to *Archaeopteryx* as "little more than a progressive and rather specialized theropod." Thulborn and Hamley (1982) repeatedly questioned the assumption that *Archaeopteryx* was a bird. Finally, Thulborn (1984) presented a cladogram (Fig. 15) in which *Archaeopteryx* is only a moderately derived theropod, and tyrannosaurids, a troodontid-ornithomimid clade, and *Avimimus* are successively closer out-groups of true birds. Similar views were expressed by Paul (1984), whose cladistic analysis concluded that *Archaeopteryx* was an early member of a "protobird" lineage, and that dromaeosaurids, caenagnathids, and troodontids are successively closer to birds (Fig. 14). In fact, Paul (1984:179) went so far as to propose that "dromaeosaurs are probably ground dwelling descendents of the flying archaeopterygids." Paul (1988a) reiterated this claim and expanded his argument in his book on theropods (Paul, 1988b), in which he placed *Avimimus* as the sister-group of true birds.

Avimimus deserves a great deal of attention because it displays a large number of avian features throughout the skeleton. As mentioned, Thulborn (1984) and Paul (1988b) placed *Avimimus* as the sister-taxon of birds (excluding *Archaeopteryx*), and Molnar and Archer (1984) placed it within Aves (including *Archaeopteryx*). Molnar (1985) reevaluated the characters of *Avimimus* and found it more "birdlike" than *Archaeopteryx* but lacking in some of the avian characters (e.g., furcula, opisthopubis) of other theropods. The Soviet paleornithologist Kurochkin (1985) interpreted the significance of *Avimimus* as demonstrating a common "evolutionary potential" among birds and theropods, and supports (in agreement with Paul) the origin of some theropods from *Archaeopteryx* rather than the origin of birds from theropods. Barsbold (1983) also envisioned a great deal of convergence within theropods—a process he termed "ornithization." Barsbold viewed several lineages as becoming birdlike, with *Archaeopteryx* simply representing one of these "ornithized" clades. Kurzanov (1985, 1987), the Soviet paleontologist who first described *Avimimus*, regarded it as feathered (on the basis of an ulnar ridge and elbow kinematics) and perhaps even volant. With respect to avian origins, however, Kurzanov agreed with Kurochkin and Barsbold that convergent evolution of birdlike features within theropods has been widespread, which confounds our efforts to determine the true ancestry of birds. Kurzanov also can be added to the list of those stripping *Archaeopteryx* of its avian status. Kurzanov acknowledged that *Avimimus* may be

close to birds but concluded (1985:98) that "the ancestors of the birds are to be found, if not among the theropod dinosaurs, at least within an ancestral group of the theropods."

Kurzanov is not alone among theropod workers in arguing that a Triassic origin of birds is possible. Raath (1985) suggested that *Archaeopteryx* (and all birds) were descended from Triassic "procompsognathid" theropods similar to *Syntarsus* (Fig. 17). Raath (1985) indeed demonstrated a number of similarities between *Syntarsus* and *Archaeopteryx*, but his analysis did not incorporate other taxa, and he was not explicit about character polarities. Chatterjee (1987a) agreed with Raath that these early theropods may be closer than the Cretaceous maniraptorans to avian origins. This hypothesis has the advantage that the theropod sister-group is actually earlier in time than *Archaeopteryx* but must invoke a great deal of convergence. It is yet another hypothesis awaiting a more complete phylogenetic exposition.

CONCLUSIONS

The origin of birds has fascinated scientists since the discovery of *Archaeopteryx* and *Compsognathus*. These fossils helped bridge the gap that confounded nearly all earlier thinkers. The near coincidence of the descriptions of these fossils and the publication of Darwin's *Origin* virtually assured the debate on avian origins a prominent place in the new evolutionary controversy. The list of scientists who published on the topic includes many of the most important paleontologists of all time: Huxley, Owen, Seeley, Haeckel, Gegenbaur, Dollo, Cope, Marsh, Williston, Osborn, Abel, Broom, Nopsca, Gregory, de Beer, and Simpson. Even today, publications on the subject appear regularly. In fact, the number of bird origin papers published since 1970 far outstrips the total number from all previous years.

It is tempting to believe that even without *Archaeopteryx* and *Compsognathus*—armed only with Darwin's theory of common descent—Huxley, Gegenbaur, or Haeckel might have reached similar insights into the origin of birds. But the history of the debate has been characterized by the formulation of new ideas as a result of the discovery of new fossils. The discovery of *Archaeopteryx* and *Compsognathus* resulted in the dinosaurian hypothesis, the discovery of *Euparkeria* produced the pseudosuchian hypothesis, and the discovery of *Deinonychus* was the stimulus for the coelurosaurian hypothesis. Recent finds of small theropods such as *Troodon* and *Avimimus* and primitive archosaurs such as *Longisquama* and *Megalancosaurus* offer prospects of new ideas for the future. Very intriguing are reports of fossil birds from the Triassic of Texas (Chatterjee,

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