

# THE MESOZOIC RADIATION OF BIRDS

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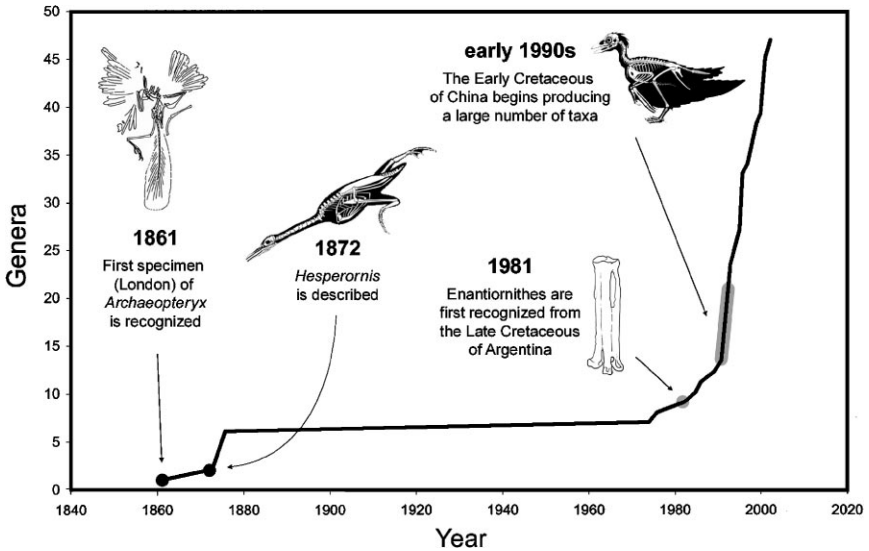
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■ **Abstract** Until recently, most knowledge of the early history of birds and the evolution of their unique specializations was based on just a handful of diverse Mesozoic taxa widely separated in time and restricted to marine environments. Although *Archaeopteryx* is still the oldest and only Jurassic bird, a wealth of recent discoveries combined with new phylogenetic analyses have documented the divergence of a number of lineages by the beginning of the Cretaceous. These and younger Cretaceous fossils have filled much of the morphological chasm that existed between *Archaeopteryx* and its living counterparts, providing insights into the evolutionary development of feathers and other important features of the avian flight system. Dramatic new perceptions of the life history, growth and development of early birds have also been made possible by the latest data. Although no primitive birds are known to have survived beyond the end of the Cretaceous, the present fossil record provides no evidence for a sudden disappearance. Likewise, a Mesozoic origin for extant birds remains controversial.

## INTRODUCTION

Birds are the most speciose group of land vertebrates. Today's 10,000 species are the extant members of an ancient radiation that can be traced back 150 million years, to the famous *Archaeopteryx lithographica* from the Late Jurassic Solnhofen limestones of Germany. The taxonomic diversity and genealogical relationships of early birds, the origin and refinement of flight, the timing of divergence of extant lineages, and the origin of avian functional and physiological specializations are just some of the evolutionary issues that have captured the interest of decades of paleornithological research. For most of this time, evidence for investigating these issues was limited to a small number of fossils greatly separated both temporarily and morphologically, and largely restricted to near-shore and marine environments. This situation has continued to change over the past two decades, as increasing discoveries of Cretaceous birds have begun to reveal an unexpected diversity of lineages (Figure 1). The number of new species of Mesozoic birds discovered and described over the past 10 years more than triples those known for much of the past



**Figure 1** Descriptions of non-neornithine bird genera over time. Note the steep increment of new discoveries during the past two decades.

two centuries (Table 1). This burst of fossil discoveries has been summarized in a number of recent publications (Chiappe 1995, Chatterjee 1997, Padian & Chiappe 1998, Feduccia 1999). Although essentially examining the same fossil record, these studies reveal a variety of interpretations resulting from different methodological approaches to reconstructing phylogeny. Our review is one guided by the principles of phylogenetic systematics.

## ORIGINS

The origin of birds—Aves, the clade including the last common ancestor of *Archaeopteryx* and living birds—has been the subject of debate almost since the advent of evolutionary thought. Historical proposals for the ancestry of birds have included turtles, lizards, crocodylomorphs, and pterosaurs, as well as both ornithischian and theropod dinosaurs (Witmer 1991, Padian & Chiappe 1998). Today, in spite of a few remaining and poorly substantiated hypotheses identifying crocodiles (Martin 1983, Martin et al. 1980, Martin & Stewart 1999) or a variety of basal archosauromorphs (Feduccia & Wild 1993, Welman 1995) as birds' closest relatives, most researchers agree that birds are theropod dinosaurs (Chatterjee 1997, Chiappe 2001, Gauthier & Gall 2001). Although this idea had its roots in the nineteenth century, modern hypotheses stem from the detailed work of J. Ostrom (1969, 1973, 1976). Since then, a wealth of osteological evidence has accumulated in support of Ostrom's hypothesis that birds originated within small and predominantly terrestrial coelurosaurian theropods (Ostrom 1976;

**TABLE 1** Described genera of Mesozoic birds (those of questionable validity are not listed). Environment and year refer to the depositional environment and year of original description, respectively; taxonomic position of *Rathonavis ostromi* follows Forster et al. 1998a

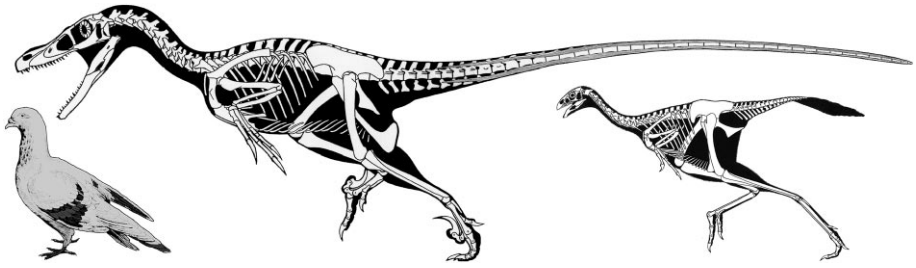
Genera	Clade	Stratigraphic age	Material	Environment	Distribution	Year
<i>Archaeopteryx</i>	Archaeopterygidae	L. Jurassic	Several specimens	Near shore	Germany	1861
<i>Rathonavis</i>	Archaeopterygidae	L. Cretaceous	Single specimen	Inland	Madagascar	1998
<i>Confuciusornis</i>	Confuciusornithidae	E. Cretaceous	Many specimens	Inland	China	1995
<i>Changchengornis</i>	Confuciusornithidae	E. Cretaceous	Single specimen	Inland	China	1999
<i>Nanantius</i>	Enantiornithes	E. Cretaceous	Isolated bones	Near shore	Australia	1986
<i>Noguerornis</i>	Enantiornithes	E. Cretaceous	Single specimen	Inland	Spain	1989
<i>Iberomesornis</i>	Enantiornithes	E. Cretaceous	Single specimen	Inland	Spain	1992
<i>Sinornis</i>	Enantiornithes	E. Cretaceous	Several specimens	Inland	China	1992
<i>Otognomis</i>	Enantiornithes	E. Cretaceous	Single specimen	Inland	China	1994
<i>Boluoichia</i>	Enantiornithes	E. Cretaceous	Single specimen	Inland	China	1995
<i>Concornis</i>	Enantiornithes	E. Cretaceous	Single specimen	Inland	Spain	1995
<i>Eoalulavis</i>	Enantiornithes	E. Cretaceous	Single specimen	Inland	Spain	1996
<i>Eoenantiornis</i>	Enantiornithes	E. Cretaceous	Single specimen	Inland	China	1999
<i>Propteryx</i>	Enantiornithes	E. Cretaceous	Single specimen	Inland	China	2000
<i>Gobipteryx</i>	Enantiornithes	L. Cretaceous	Several specimens	Inland	Mongolia	1974
<i>Alexornis</i>	Enantiornithes	L. Cretaceous	Isolated bones	Inland	Mexico	1976
<i>Enantiornis</i>	Enantiornithes	L. Cretaceous	Isolated bones	Inland	Argentina	1981
<i>Avisaurus</i>	Enantiornithes	L. Cretaceous	Isolated bones	Inland	USA	1985
<i>Soroavisaurus</i>	Enantiornithes	L. Cretaceous	Isolated bones	Inland	Argentina	1993
<i>Yungavolucris</i>	Enantiornithes	L. Cretaceous	Isolated bones	Inland	Argentina	1993

(Continued)

TABLE 1 (Continued)

Genera	Clade	Stratigraphic age	Material	Environment	Distribution	Year
<i>Lectavis</i>	Enantiornithes	L. Cretaceous	Isolated bones	Inland	Argentina	1993
<i>Neuquenornis</i>	Enantiornithes	L. Cretaceous	Single specimen	Inland	Argentina	1994
<i>Halmimornis</i>	Enantiornithes	L. Cretaceous	Single specimen	Offshore	USA	2002
<i>Enaliornis</i>	Ornithuromorpha	E. Cretaceous	Isolated bones	Offshore	UK	1876
<i>Ambiortus</i>	Ornithuromorpha	E. Cretaceous	Single specimen	Inland	Mongolia	1982
<i>Gansus</i>	Ornithuromorpha	E. Cretaceous	Single specimen	Inland	China	1984
<i>Longipteryx</i>	Ornithuromorpha	E. Cretaceous	Single specimen	Inland	China	2001
<i>Yanornis</i>	Ornithuromorpha	E. Cretaceous	Single specimen	Inland	China	2001
<i>Yixianornis</i>	Ornithuromorpha	E. Cretaceous	Single specimen	Inland	China	2001
<i>Hesperornis</i>	Ornithuromorpha	L. Cretaceous	Many specimens	Offshore	USA/Canada	1872
<i>Ichthyornis</i>	Ornithuromorpha	L. Cretaceous	Many specimens	Offshore	USA/Canada	1872
<i>Apatornis</i>	Ornithuromorpha	L. Cretaceous	Single specimen	Offshore	USA	1876
<i>Baptornis</i>	Ornithuromorpha	L. Cretaceous	Several specimens	Offshore	USA/Canada	1877
<i>Parahesperornis</i>	Ornithuromorpha	L. Cretaceous	Single specimen	Offshore	USA	1984
<i>Patagopteryx</i>	Ornithuromorpha	L. Cretaceous	Several specimens	Inland	Argentina	1992
<i>Vorona</i>	Ornithuromorpha	L. Cretaceous	Single specimen	Inland	Madagascar	1996
<i>Limenavis</i>	Ornithuromorpha	L. Cretaceous	Single specimen	Inland	Argentina	2001
<i>Apsaravis</i>	Ornithuromorpha	L. Cretaceous	Single specimen	Inland	Mongolia	2001
<i>Chaoyangia</i>	Controversial status	E. Cretaceous	Single specimen	Inland	China	1995
<i>Liaoningornis</i>	Controversial status	E. Cretaceous	Single specimen	Inland	China	1996
<i>Sapeornis</i>	Controversial status	E. Cretaceous	Single specimen	Inland	China	2002

Abbreviations: E., Early; L., Late.



**Figure 2** Reconstructions of the dromaeosaurid *Velociraptor mongoliensis* (left; after Paul 1988) and the oviraptorosaur *Caudipteryx zoui* (right; after Currie 2000) scaled to a rock pigeon (*Columba livia*).

Gauthier 1986; Holtz 1998, 2001; Sereno 1999; Norell et al. 2001) (Figure 2). Alternative hypotheses, however, compete regarding the exact sister-taxon of Aves among coelurosaurians, with dromaeosaurids (e.g., *Deinonychus*, *Velociraptor*, *Sinornithosaurus*), troodontids (e.g., *Troodon*, *Byronosaurus*), oviraptorids (e.g., *Oviraptor*, *Khan*), and alvarezsaurids (e.g., *Mononykus*, *Shuvuuia*), being commonly cited (Ostrom 1976; Gauthier 1986; Perle et al. 1993a, 1994; Holtz 1998, 2001; Sereno 1999; Chiappe et al. 1996, 1998; Elzanowski 1999; Xu et al. 1999b, 2000; Norell et al. 2001).

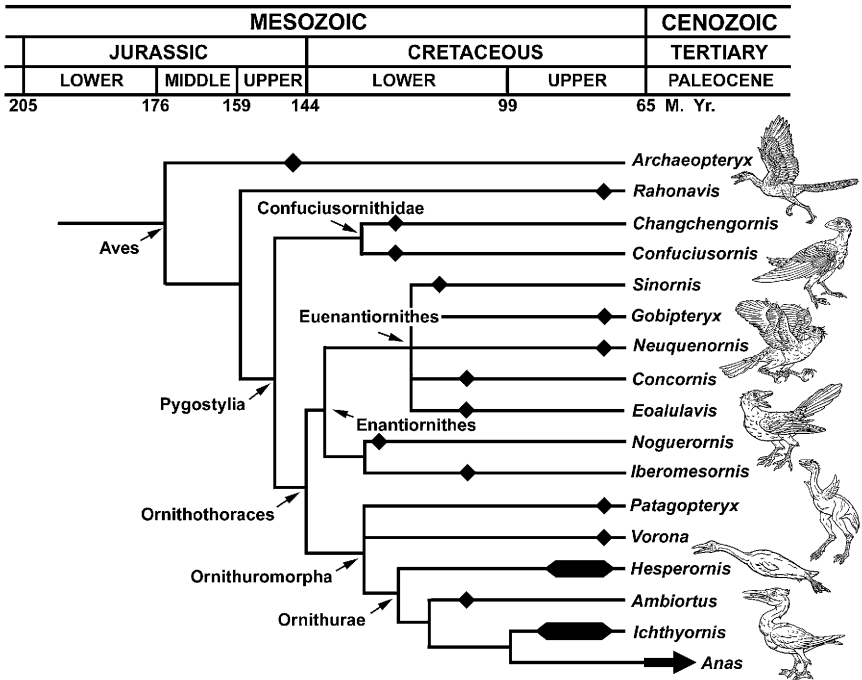
For decades, interpretation of birds as living dinosaurs was based on osteological comparisons, but a series of recent discoveries have provided additional evidence in support of this hypothesis (Chiappe 2001). Discoveries of embryonic remains of coelurosaurians inside their eggs have provided evidence of the egg morphology of theropod dinosaurs (Norell et al. 1994, Varricchio et al. 1997) and have shown that features of the shell microstructure are uniquely shared between birds and these non-avian theropod lineages (Grellet-Tinner & Chiappe, 2002). Specimens associating adult coelurosaurians with their clutches of eggs have allowed for inferences of nesting behavior and suggest the presence of avian brooding behavior among these dinosaurs (Norell et al. 1995, Dong & Currie 1996, Varricchio et al. 1997, Clark et al. 1999). Finally, a number of exquisitely preserved coelurosaurians from the Early Cretaceous of China (Chen et al. 1998; Ji et al. 1998; Xu et al. 1999b, 2000, 2001; Zhou & Wang 2000; Zhou et al. 2000; Norell et al. 2002) have compellingly shown that feathers had their origin within theropod dinosaurs. This wealth of data accumulated over decades of osteological research and recently corroborated by studies of oology, behavior, and integument, suggests beyond any reasonable doubt that birds evolved from coelurosaurian dinosaurs sometime before the Late Jurassic. However, the temporal context for this divergence hinges upon identifying the oldest records for the group.

For much of the history of paleornithology, the Late Jurassic *Archaeopteryx* stood unchallenged as the oldest known bird. In recent years, however, several alleged fossil birds have been claimed to be older than this taxon, although none



**Figure 3** Reconstruction of the controversial *Protoavis texensis* from the Late Triassic of Texas (after Chatterjee 1999) scaled to a rock pigeon (*Columba livia*). In spite of comprehensive reconstructions such as this, the known material of this taxon is extremely fragmentary.

has yet been proved convincingly (Molnar 1985, Chiappe 1995, Padian & Chiappe 1998). The most publicized and contentious is *Protoavis texensis* from the Late Triassic Dockum Group of West Texas (Chatterjee 1991, 1997, 1999) (Figure 3). Most of the available material of this taxon comprises two disarticulated skeletons collected in 1983 from a bone-bed (Post Quarry) that has produced a diverse array of tetrapods (Chatterjee 1997). A few more isolated bones were collected years later from another site (Kirkpatrick Quarry) some 50 km away and 60 m lower than, Post Quarry (Chatterjee 1999). Because *Protoavis* is more than 75 million years older than *Archaeopteryx* and supposedly a member of Ornithothoraces (Figure 4) (Chatterjee 1991, 1999), acceptance of this taxon as a bird would mean that the origin of the group would have to have occurred deep in the Triassic, if not earlier. Yet the available material of *Protoavis* is problematic. The poor preservation of several elements precludes their osteological identification and a number of features have been misinterpreted (Chiappe 1998, Witmer 2001). Some of the additional material from Kirkpatrick Quarry—in particular a large keeled bone interpreted as a sternum (Figure 3)—does not overlap with either the type or referred specimen from Post Quarry, thus rendering impossible their referral to *Protoavis*. Even the placement of these specimens within a single species has been questioned (Ostrom 1991, Chiappe 1998, Renesto 2000, Sereno 2000, Witmer 2001), which some believe to be a composite formed by disparate taxa (Sereno 2000, Witmer 2001). Although it is true that the issue to be addressed is not whether the skeletons of *Protoavis* are made of several disparate taxa but rather whether any of those bones are avian (Witmer 1997, 2001), such a conclusion should



**Figure 4** Phylogenetic relationships of principal lineages of Mesozoic birds (after Chiappe 2001).

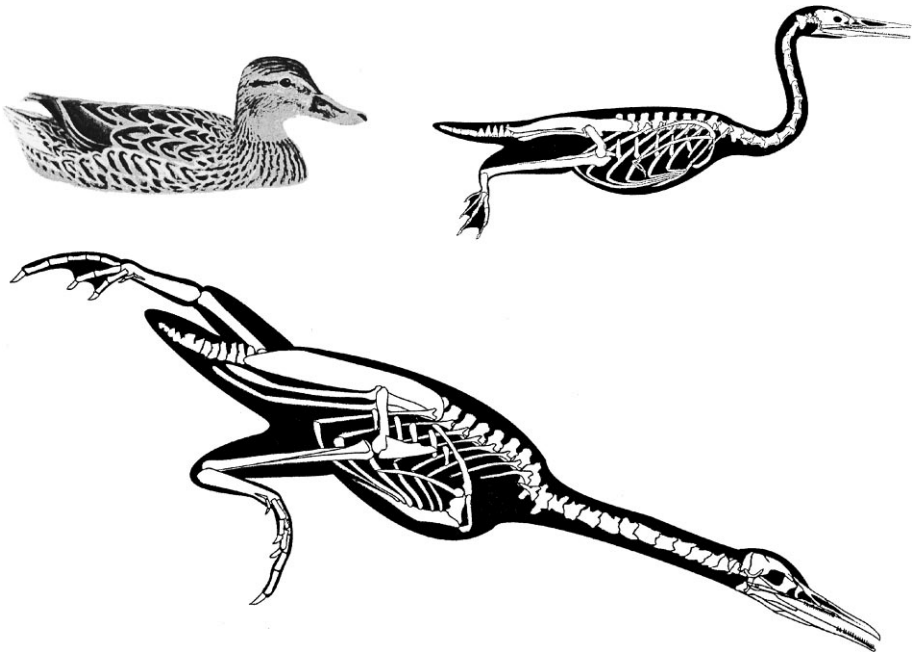
be supported by a cladistic analysis, difficult to perform with incomplete single bones (Clarke & Chiappe 2001). Interestingly, one of the most compelling avian features of *Protoavis*, the near-heterocoelic (saddle-shaped) cervical vertebrae, has recently been reported for *Megalancosaurus preonensis*, a chameleon-bodied diapsid reptile of uncertain relationships (Renesto 2000), but also from the Late Triassic.

No reliable evidence has yet come to light in support of the existence of fossil birds prior to the Late Jurassic; *Archaeopteryx lithographica* remains the oldest known and most primitive bird. Eight skeletal specimens and a feather (Mäuser 1997, Elzanowski 2002) presumed to belong to this taxon are in existence but in spite of their spectacular preservation, only limited anatomical information is available for certain areas of the skeleton (e.g., braincase, palate, orbit, sternum, feet). Even the placement of these specimens in one or more closely related species remains controversial. Although new names have occasionally been applied to some of them (e.g., Howgate 1984, Wellnhofer 1993, Elzanowski 2001), support for the existence of another bird as well as *Archaeopteryx lithographica* in the Solnhofen limestones remains unconvincing. The most debated aspect of this bird, however, concerns its mode of life. Was it predominantly arboreal or terrestrial? Did

it climb trees using its forelimbs? Could it fly, and if so, how well? Was it a “glider” or a “flapper”? Although numerous and diverse hypotheses have been proposed for these and other ecological and functional questions (Padian & Chiappe 1998), they remain conjectural and are unlikely ever to be tested. At this point, we concur with functional and aerodynamic considerations that interpret *Archaeopteryx* as a predominantly terrestrial bird (Ostrom 1974, Chiappe 1995), able to take off from the ground (Burgers & Chiappe 1999) and to fly by flapping its asymmetrically feathered wings (Rayner 2001).

## BASAL LINEAGES

For almost a century, knowledge of the Cretaceous diversity of birds was limited to a series of fossils from the marine deposits of the Late Cretaceous Western Interior Seaway of North America. Although toothed, these ichthyornithiforms and hesperornithiforms (Figure 5) were distinctly modern in many aspects of their skeletons (Marsh 1880), a fact noticed by early studies that placed them either close to recent birds (Heilmann 1926) or as basal forms of different extant lineages (Marsh 1880, Brodkorb 1971, Simpson 1980). The morphology of *Hesperornis* and *Ichthyornis* testified to an enormous gap in the early history of the group when



**Figure 5** Reconstructions of the marine ornithurine birds *Hesperornis regalis* (bottom) and *Baptonis advenus* (top right) scaled to a mallard (*Anas platyrhynchos*).

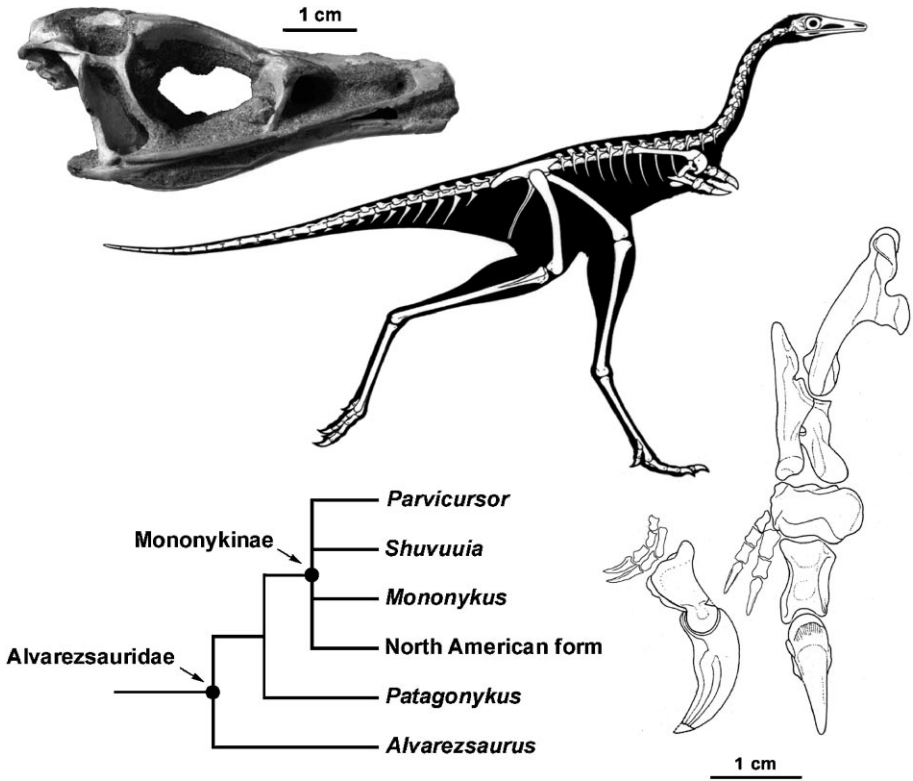


compared to the much older *Archaeopteryx*. Many of the discoveries of recent years have served to fill in this morphological and temporal gap and now more than 30 valid avian taxa, representing different intermediate lineages, have been recognized from the Mesozoic (Table 1). Conversely the fossil record of birds close to the divergence of the extant lineages (Neornithes) has remained largely unchanged (Norell & Clarke 2001).

## Cretaceous Diversity

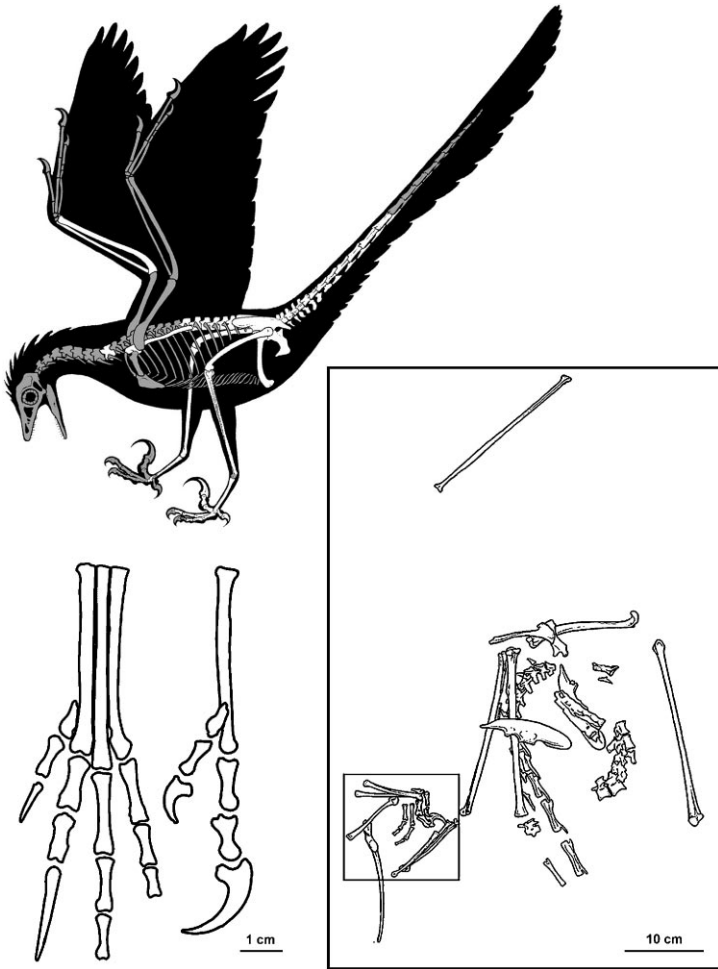
Much recent controversy surrounded the discovery of two Late Cretaceous lineages claimed to be only slightly more advanced than *Archaeopteryx*: alvarezsaurids (Figure 6) and *Rahonavis ostromi* (Figure 7). Alvarezsaurids were first recognized in 1991 on the basis of an incomplete specimen from Patagonia, named *Alvarezsaurus calvoi* and interpreted as an enigmatic non-avian theropod (Bonaparte 1991). The subsequent discovery of *Mononykus olecranus* (Perle et al. 1993a,b) from the Gobi Desert (Figure 6), a long-legged cursor with short and stout forelimbs, and a multi-toothed and highly kinetic skull (Perle et al. 1994, Chiappe et al. 1998), shed much light both on the bird-like osteology and phylogenetic position of the group. Nonetheless, the close relationship between *Alvarezsaurus* and *Mononykus* was not recognized until the discovery of the Patagonian *Patagonykus puertai* (Novas 1996, 1997). Since then other fossil discoveries as well as new taxa have documented that alvarezsaurids were a diverse group of agile cursors inhabiting South and North America as well as Central Asia (Chiappe et al. 2002a). In spite of the superficially non-avian morphology of the abbreviated forelimb of *Mononykus*, initial cladistic analyses (Perle et al. 1993a, Chiappe et al. 1996, Novas 1996) interpreted it to be phylogenetically closer to extant birds than *Archaeopteryx*. This "avian hypothesis" immediately resulted in a great deal of opposition (Martin & Rinaldi 1994, Ostrom 1994, Wellnhofer 1994, Zhou 1995a, Feduccia & Martin 1996), although dissent was not framed in a cladistic context (Chiappe et al. 2002a). Studies of additional fossils and cladistic analyses following that of Perle et al. (1993a) consolidated the avian relationship of the group (Chiappe et al. 1996, 1998; Novas 1996, 1997; Forster et al. 1998a; Holtz 1998, 2001). The "avian hypothesis" received further support when structures found surrounding a skeleton of the Asian alvarezsaurid *Shuvuuia deserti* were immunologically shown to be composed of only  $\beta$ -keratin (Schweitzer et al. 1999), just like the feathers of birds (Brush 2001). However, given the subsequent discovery of feathers in non-avian theropods, the presence of these integumentary structures in alvarezsaurids would not alone be sufficient to support their avian relationship (Schweitzer et al. 1999).

Over the past few years, however, more serious questions have been raised contrary to the "avian hypothesis." Several cladistic analyses (Serenó 1999, 2000, 2001; Chiappe 2002a; Norell et al. 2001; Clark et al. 2002; Novas & Pol 2002) have argued for a non-avian relationship of alvarezsaurids, resulting in different placements of the group within coelurosaurian theropods. Whereas Sereno (1999,



**Figure 6** Alvarezsaurids are known by five described Late Cretaceous genera, two from southern South America (*Alvarezsaurus* and *Patagonykus*) and three from central Asia (*Mononykus*, *Shuvuuia*, and *Parvicursor*, although the last two could be synonyms), as well as a fragmentary, unnamed specimen from North America. The Asian and North American forms comprise a monophyletic group, mononykines (centered skeletal reconstruction), with the South American taxa forming successive outgroups (Novas 1996, Chiappe et al. 1998) (cladogram on lower left corner). The skull of *Shuvuuia* (top left corner) shows the apomorphic nature of the alvarezsaurid cranium, with large orbits, an elongated snout, and a prokinetic type of skull kinesis (Chiappe et al. 1998). A recently described specimen of *Shuvuuia* (Suzuki et al. 2002) has a nearly complete hand preserved in articulation that provides evidence that mononykines, and presumably all alvarezsaurids, had two manual digits (fingers 2 and 3) in addition to the stout digit 1 characteristic of the group (lower right corner).

2000), Norell et al. (2001), Clark et al. (2002), and Novas & Pol (2002) have proposed a more basal placement within theropods, Chiappe (2002a) placed alvarezsaurids as the immediate outgroup of Aves. Among the diverse non-avian hypotheses that have been put forward, Sereno's (1999, 2001) claim for a close relationship between alvarezsaurids and ornithimimid coelurosaurs (i.e., "ostrich-like" theropods) is the most radical, since under this hypothesis, alvarezsaurids



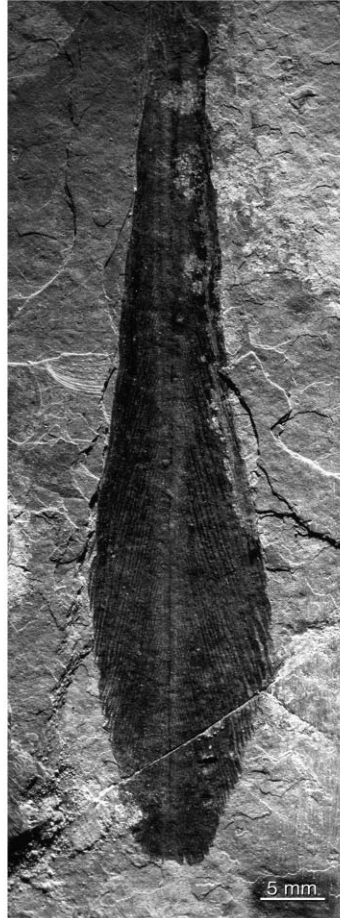
**Figure 7** The Late Cretaceous *Rahonavis ostromi* of Madagascar. Skeletal reconstruction (*top left*) of the singly known specimen of this taxon. Note the proximity in which the skeletal elements of this specimen were found (*outer box*). *Rahonavis*' sickle-clawed foot is shown in dorsal and medial views (*bottom left*). (After Forster et al. 1998a).

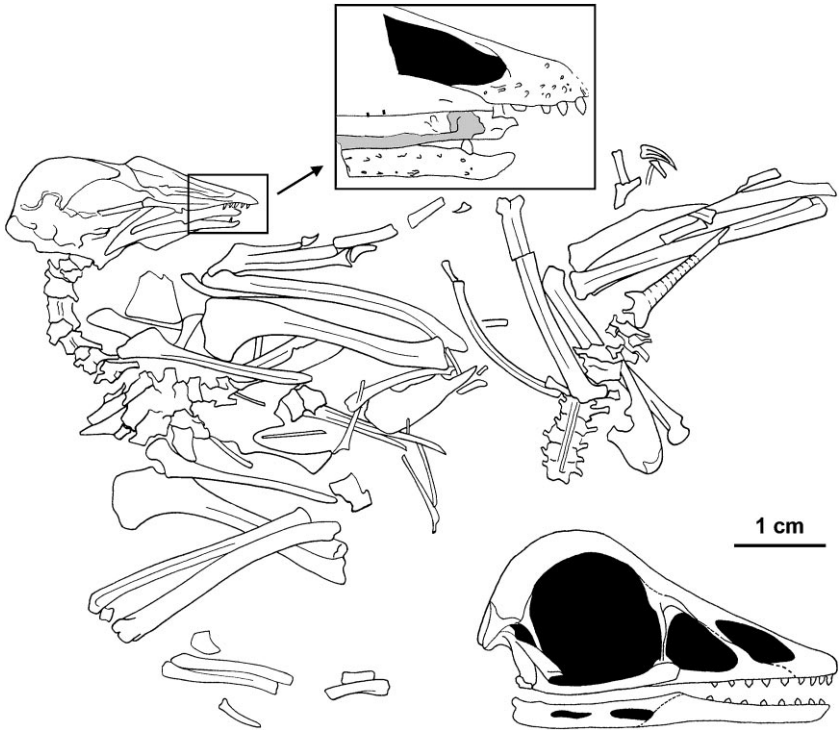
are placed outside maniraptoriforms within a new clade, the Ornithomimoidea (alvarezsaurids + ornithomimids). However, critical examination of the character evidence for this hypothesis has shown that support is, at best, weak (Suzuki et al. 2002). Although at this point the precise phylogenetic placement of alvarezsaurids within coelurosaurians remains in question, it is evident that the group has relevance for understanding the evolutionary transformations that led to the origin of extant birds.

The Malagasy *Rahonavis ostromi* (Forster et al. 1998a,b) (Figure 7) is another recently discovered basal taxon whose avian status has subsequently been challenged. On the basis of a cladistic analysis including several non-avian theropods and basal birds, Forster et al. (1998a) placed this sickle-clawed bird as the sister-taxon of *Archaeopteryx*, although cautioning about the possibility of it being closer to neornithine (extant) birds (an alternative concordant with its placement by Chiappe 2002a; see Figure 4). Combining a suite of avian features such as a reversed first toe (Figure 7) and quill knobs on the forearm with the sickle-clawed pedal specializations of dromaeosaurid theropods, *Rahonavis* provided further evidence in support of a coelurosaurian origin of birds (Forster et al. 1998a). Because of this apparently mosaic combination of characters, critics of the theropod hypothesis of avian ancestry claimed the holotype to be a composite (Feduccia 1999, Geist & Feduccia 2000): the forelimb and shoulder girdle of a bird mixed up with the hindlimb, pelvis, and tail of a non-avian theropod. Nevertheless, the taphonomic context of *Rahonavis* suggests otherwise. Although mostly disarticulated, the single specimen has no duplicated elements and was found on a surface of less than 0.14 m<sup>2</sup> (Figure 7). This alone strongly suggests that all described bones belong to a single individual (Forster et al. 1998a). Further, Forster et al. (1998a) were careful to address this issue by conducting separate cladistic analyses, one scoring the whole specimen and another excluding the forelimb and shoulder from the data set. Both analyses produced the same result, placing *Rahonavis* in a basal position within birds. Although subsequent studies also supported this basal placement for *Rahonavis* (Holtz 1998, Chiappe 2002a), more recent work by Holtz (2001) and Clark et al. (2002) have hypothesized that this taxon is the most immediate outgroup of Aves.

Although the avian relationship of Alvarezsaurids and *Rahonavis* has been hotly debated, the paramount issue within basal avian systematics remains whether or not there is a deep dichotomy separating two main evolutionary radiations, which acquired in parallel, a suite of increasingly derived (i.e., modern) characters. A number of workers (e.g., Martin 1983, 1995; Kurochkin 1995, 1996, 2000, 2001; Hou et al. 1995, 1996; Feduccia 1999) have argued that all basal lineages of birds can be classified within two major subdivisions. On the one hand, “Sauriurae” encompassing *Archaeopteryx*, Confuciusornithidae (toothless birds from the Early Cretaceous of China; Chiappe et al. 1999) (Figure 8), and Enantiornithes (a flighted, cosmopolitan group recorded throughout the Cretaceous; Chiappe & Walker 2002) (Figure 9), and on the other hand, the Ornithurae, including several lineages of Cretaceous birds (Hesperornithiformes and Ichthyornithiformes

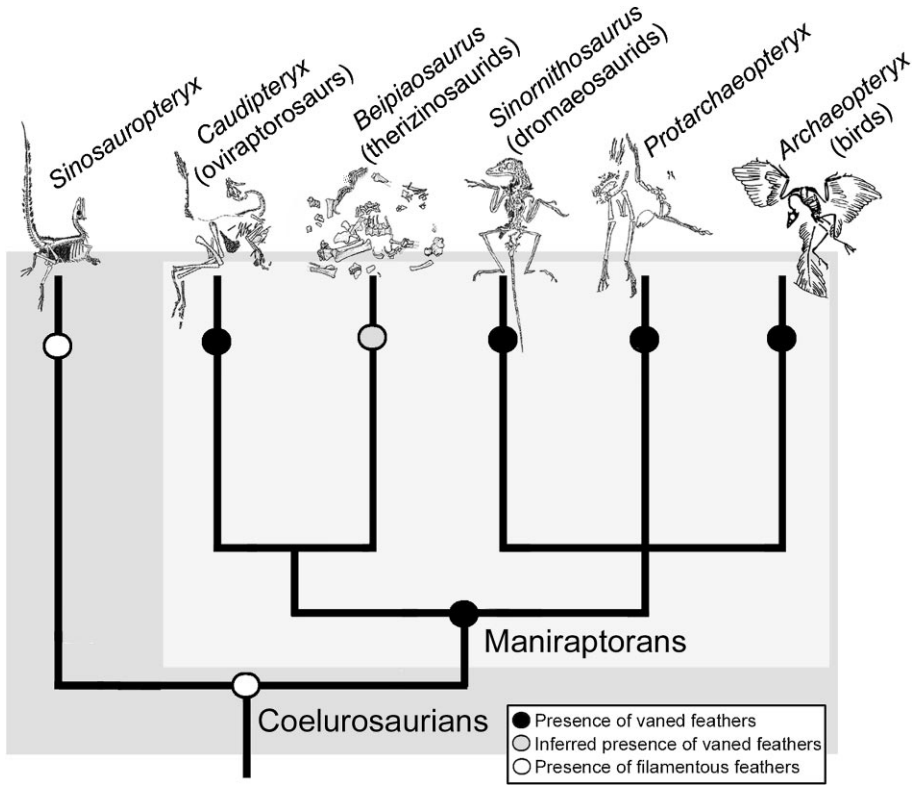
**Figure 8** The Early Cretaceous *Confuciusornis sanctus* of China. Skeletal reconstruction of this crow-sized bird (*top*). Specimen displaying a pair of long tail feathers (*bottom left*) and a close up of one of these feathers (*bottom right*). Whereas specimens preserving these long tail feathers are not uncommon, whether their presence documents the existence of sexual dimorphs or not remains unclear (Chiappe et al. 1999) (after Chiappe et al. 1999).





**Figure 9** One of several known specimens of the Early Cretaceous *Sinornis santensis* of China (center) (after Hou 1997), with a close up of the tip of its rostrum (top). Skull reconstruction of an enantiornithine hatchling from the Early Cretaceous of Spain (bottom right) (after Sanz et al. 1997). Inset not to scale.

among others) (Figure 10), plus all extant taxa. Whereas most supporters of “Sauriurae” would agree on the monophyletic status of Aves, some workers have carried this view of a basal dichotomy to an extreme (Kurochkin 2001), arguing for two completely separate origins for these groups, and thus a diphyletic Aves. However, such a notion is entirely based on primitive characters not evaluated in a cladistic framework. Several cladistic analyses have strongly supported the notion that confuciusornithids and enantiornithines are successively more closely related to extant birds (i.e., Neornithes; Figure 4) and that neither of these two basal lineages shares a common ancestor with *Archaeopteryx* that is not the common ancestor of all birds (Cracraft 1986; Chiappe 1991, 1995, 2002a; Forster et al. 1998a; Sereno 1999). Acceptance of a monophyletic “Sauriurae” requires explaining the numerous morphological and functional similarities seen between the “sauriurine” lineages (in particular Enantiornithes) and extant birds as evolutionary convergences. Parsimony analyses show, however, that these shared features are most simply explained as a stepwise series of synapomorphies diagnosing nodes within



**Figure 10** The phylogenetic distribution of the feathered coelurosaurians *Sinosauropteryx prima*, *Caudipteryx zoui*, *Beipiaosaurus inexpectus*, *Sinornithosaurus milleni*, and *Protarchaeopteryx robusta* (phylogenetic relationships simplified from Chen et al. 1998, Ji et al. 1998, and Norell et al. 2001). We agree with a number of previous studies (e.g., Ji et al. 1998, Sereno 1999, Norell et al. 2001, Clark et al. 2002) in regarding the undeniably feathered *Caudipteryx* as a non-avian coelurosaurian, specifically a member of Oviraptorosauria. Filamentous and vaned feathers are interpreted as coelurosaurian and maniraptoran synapomorphies, respectively.

a pectinate cladogram (Figure 4). The conceptual impasse underlying this phylogenetic disagreement likely resides in how workers have chosen to formulate and test homology (Chiappe 1999).

By far the most diverse group of Cretaceous birds was Enantiornithes, with nearly 20 valid species reported to date (Table 1; Figure 9) (Chiappe & Walker 2002). Basal members of this lineage are well represented in Early Cretaceous lake deposits of Spain (Sanz et al. 1995, 1996, 1997) and China (Zhou 1995b, Zhang & Zhou 2000, Zhang et al. 2001). These early enantiornithines are toothed and of small size (from that of a sparrow to that of a thrush). Their flight apparatus

approaches that of their living counterparts in proportions and shares with them several derived characters (e.g., alula, mobile scapulocoracoid articulation, narrow interclavicular). In spite of the fact that definitive evidence for perching is lacking in more basal birds, these capabilities were clearly present among the earliest enantiornithines as evidenced by their pedal morphology (Sereno & Rao 1992, Chiappe & Calvo 1994, Chiappe 1995, Martin 1995, Sanz et al. 1995, Zhou 1995b). There is a distinct size increment between these taxa and later enantiornithines such as the Late Cretaceous *Enantiornis* (with a wing-span of about 1 m; Walker 1981, Chiappe 1996), *Avisaurus* (Chiappe 1993), and *Gobipteryx* (Chiappe et al. 2001), the only known toothless member of the group. Although mostly recorded from inland deposits, enantiornithines also occupied littoral and marine environments, and even extended into polar regions (Chiappe 1996).

A number of other taxa, including one of the earliest secondarily flightless birds, the Late Cretaceous *Patagopteryx deferrariisi* from southern Argentina (Alvarenga & Bonaparte 1992, Chiappe 2002b), fall between the enantiornithine radiation and the divergence of another major group, Ornithurae, which contains the most immediate outgroups of extant birds (Figure 4). The record of these close relatives of Neornithes is mostly limited to the familiar Hesperornithiformes and Ichthyornithiformes. Hesperornithiforms comprise several species of toothed and highly specialized divers with extremely abbreviated forelimbs (Figure 5). Although primarily known from marine environments, some fossils have been recovered from estuarine and near shore deposits. Some of the most derived members (e.g., *Hesperornis regalis*) would have been about the size of an Emperor Penguin. The flighted ichthyornithiforms are represented by a handful of incompletely known taxa from essentially the same deposits as the hesperornithiforms. A revision of ichthyornithiforms has begun to cast doubts on the monophyly of this group as well as the validity of some species of *Ichthyornis* (Clarke 1999, 2002). In spite of being toothed, *Ichthyornis* and allies are morphologically very similar to their extant relatives, and although among the earliest discovered Mesozoic birds, many aspects of their anatomy, taxonomy, and inter-relationships remain unclear. One significant recent addition to the Mesozoic record of ornithurines is the exquisitely preserved *Apsaravis ukhaana* (Norell & Clarke 2001) from the Mongolian Late Cretaceous that adds critical data to understanding evolutionary transformations leading to the modern avian wing. Other recently described ornithurines include the Early Cretaceous *Yanornis martini* and *Yixianornis grabaui* from China (Zhou & Zhang 2001), which although only preliminarily studied appear to be the earliest informative members of this lineage. Finally, despite several reports of Cretaceous fossils of extant avian lineages, the existence of neornithine birds in pre-Tertiary times remains dubious (Dyke 2001).

## Do Feathers Make a Bird?

Under the accepted phylogenetic definition of Aves (i.e., common ancestor of *Archaeopteryx*, extant birds and all descendants), the existence of a suite of differentiated and structurally modern feather types (e.g., primary and secondary



remiges, retrices, and covertors) in *Archaeopteryx* strongly suggests that the origin of feathers predated the origin of birds (Serenó 1999, Rayner 2001). Recently, this prediction has been confirmed by a number of discoveries from the Early Cretaceous of China including at least six taxa of non-avian theropod dinosaurs preserving integumentary structures interpreted as feather homologues (Chen et al. 1998; Ji et al. 1998; Xu et al. 1999a,b, 2000, 2001; Norell et al. 2002). These new taxa, of a wide range of morphologies and sizes, represent lineages phylogenetically spread throughout the non-avian coelurosaurian portion of the theropod tree (Figure 10). Often preserved associated with the integumentary covering of the skull, axial and appendicular skeleton, these structures range from simple and filament-like (e.g., *Sinosauropteryx*; Chen et al. 1998, Prum 1999) to tufts joined at their bases or serially arranged along a central filament (e.g., *Sinornithosaurus*; Xu et al. 2001) to more complex structures with vanes and distinct shafts (*Caudipteryx*, *Protarchaeopteryx*; Ji et al. 1998, Zhou et al. 2000). Support for the homologous interpretation of these structures as feathers comes from their complex branched arrangement, characteristic of avian feathers (Prum 1999, Xu et al. 2001, Norell et al. 2002). Dissenters to the theropod hypothesis of bird origins have countered by claiming that in some instances these structures are not feathers but frayed internal composite fibers of the structural protein collagen (Feduccia 1999, Geist & Feduccia 2000). In other cases they have argued that the implicated taxa (e.g., *Caudipteryx* and *Protoarchaeopteryx*) are avian (Feduccia 1999, Geist & Feduccia 2000, Jones et al. 2000, Martin & Czerkas 2000, Ruben & Jones 2000), and thus irrelevant for understanding the origin of feathers. The morphology and length of the filaments, however, are inconsistent with their interpretation as frayed internal composite fibers (Prum 1999, Xu et al. 2001) and there is no doubt that these structures are external. Equally well supported is the non-avian identification of taxa for which integumentary structures have been unquestionably identified as vanned feathers, such as *Caudipteryx* and *Protarchaeopteryx* (Ji et al. 1998). Jones et al. (2000) compared the hindlimb proportions and position of the gravity center of *Caudipteryx* to those of non-avian theropods and living flightless birds, concluding that this taxon is more similar to extant flightless birds than it is to non-avian theropods. This claim remains unsubstantiated, however, since the majority of the specimens used in this study are too incompletely preserved to allow the measurements cited to be replicated and in some instances (e.g., *Carnotaurus*) the given measurements are for elements that simply do not exist. Most significantly, qualitative osteological data prevents placing both *Caudipteryx* and *Protarchaeopteryx* among birds, as shown by several recent cladistic analyses (Ji et al. 1998, Holtz 1998, Sereno 1999, Xu et al. 2000, Norell et al. 2001, Clark et al. 2002). Whereas the phylogenetic placement within the non-avian coelurosaurian tree of the incomplete *Protarchaeopteryx* remains controversial (Ji et al. 1998), the much better represented *Caudipteryx* has been consistently nested within oviraptorosaurs (Holtz 1998, Sereno 1999, Clark et al. 2001, Norell et al. 2001) (Figure 10). Morphological arguments in favor of an avian placement of *Caudipteryx* have relied on characters that are either incorrect, circular, or also found among other non-avian coelurosaurians (Table 2). A number of other characters are ambiguous because

**TABLE 2** Our interpretation of the characters used to argue for an avian rather than an oviraptorid relationship for the feathered *Caudipteryx*

**Character/interpretation**

1. **Shortened, incipiently fused tail (“protopygostyle”)** (Geist & Feduccia 2000, Martin & Czerkas 2000).  
**Irrelevant.** This character is absent in *Caudipteryx*. The distalmost tail vertebrae are fused in other oviraptorids (Barsbold et al. 2000).
2. **Ventrally oriented foramen magnum** (Geist & Feduccia 2000).  
**Ambiguous.** The known skulls of *Caudipteryx* are not well enough preserved to identify the orientation of the foramen magnum (Ji et al. 1998).
3. **Vaned feathers** (Geist & Feduccia 2000, Martin & Czerkas 2000).  
**Circular.** This character cannot be used in favor of the avian relationship of *Caudipteryx* since the hypothesis to be tested is that vaned feathers occur in non-avian theropods.
4. **Ligamental quadratojugal-quadratoarticular articulation** (Geist & Feduccia 2000, Ruben & Jones 2000).  
**Ambiguous.** The preservation of the known specimens, in which pertinent bones are disarticulated, makes this character problematic.
5. **Lack of contact between quadratojugal and squamosal** (Geist & Feduccia 2000, Ruben & Jones 2000).  
**Ambiguous.** The preservation of the known specimens, in which pertinent bones are disarticulated, makes this character problematic.
6. **Absence of obturator process on ischium** (Ruben & Jones 2000).  
**Incorrect.** A distinct and large obturator process is present at least in the holotype specimen of *Caudipteryx* (Ji et al. 1998).
7. **Expanded roots on premaxillary teeth** (Martin & Czerkas 2000).  
**Ambiguous.** The teeth of *Caudipteryx* are highly apomorphic, greatly differing from both avian and non-avian theropod teeth.
8. **Carpus containing at least four bones** (Martin & Czerkas 2000).  
**Irrelevant.** Three carpals are preserved in the holotype of *Caudipteryx*, these correspond to the radiale, semilunate, and element X (Hinchliffe 1985). The ‘absence’ of an ulnare (i.e., fourth carpal), otherwise present in all tetrapods, is clearly due to a preservation bias. Four or more carpals are known for other nonavian theropods (Xu et al. 1999b).
9. **Absence of pubic foot** (Martin & Czerkas 2000).  
**Ambiguous.** The distal ends of the pubes of the known specimens of *Caudipteryx* (Ji et al. 1998; Zhou et al. 2000) are not preserved.
10. **Opposable first toe** (Martin & Czerkas 2000).  
**Incorrect.** This character cannot be confirmed in any of the known specimens of *Caudipteryx* (Z. Zhou 2001, personal communication).
11. **Loss of teeth in maxilla and mandible** (Martin & Czerkas 2000).  
**Irrelevant.** Teeth are absent in the maxilla and mandible of all oviraptorids (Barsbold et al. 1990, Clark et al. 2001) and present in most non-neornithine lineages (Chiappe et al. 1999).
12. **Mandibular foramen** (Martin & Czerkas 2000).  
**Irrelevant.** A mandibular foramen is present in most archosaurs including theropod dinosaurs.

(Continued)

TABLE 2 (Continued)

**Character/interpretation**

- 13. Enlargement of premaxilla** (Martin & Czerkas 2000).  
**Irrelevant.** An expanded premaxilla is typical of oviraptorid theropods (Barsbold et al. 1990, Clark et al. 2001).
- 14. Reduction of maxilla** (Martin & Czerkas 2000).  
**Irrelevant.** An expanded premaxilla is typical of oviraptorid theropods (Barsbold et al. 1990, Clark et al. 2001).
- 15. Reduction of hyperpubic spoon** (Martin & Czerkas 2000).  
**Ambiguous.** The distal ends of the pubes are not preserved in the known specimens of *Caudipteryx* (Ji et al. 1998, Zhou et al. 2000).
- 16. Ball-shaped head of femur** (Martin & Czerkas 2000).  
**Irrelevant.** A ball-shaped femoral head is present in all dinosaurs including oviraptorids and birds.
- 17. Reduction of fibula** (Martin & Czerkas 2000).  
**Incorrect.** A distinct socket on the calcaneum of *Caudipteryx* indicates that although the fibulae are incomplete these bones reached the proximal tarsals (Ji et al. 1998) and thus, they were not reduced.
- 18. Enlargement of astragalus at the expense of calcaneum** (Martin & Czerkas 2000).  
**Irrelevant.** A much larger astragalus than calcaneum is primitive for coelurosaurian theropods including oviraptorids and birds.

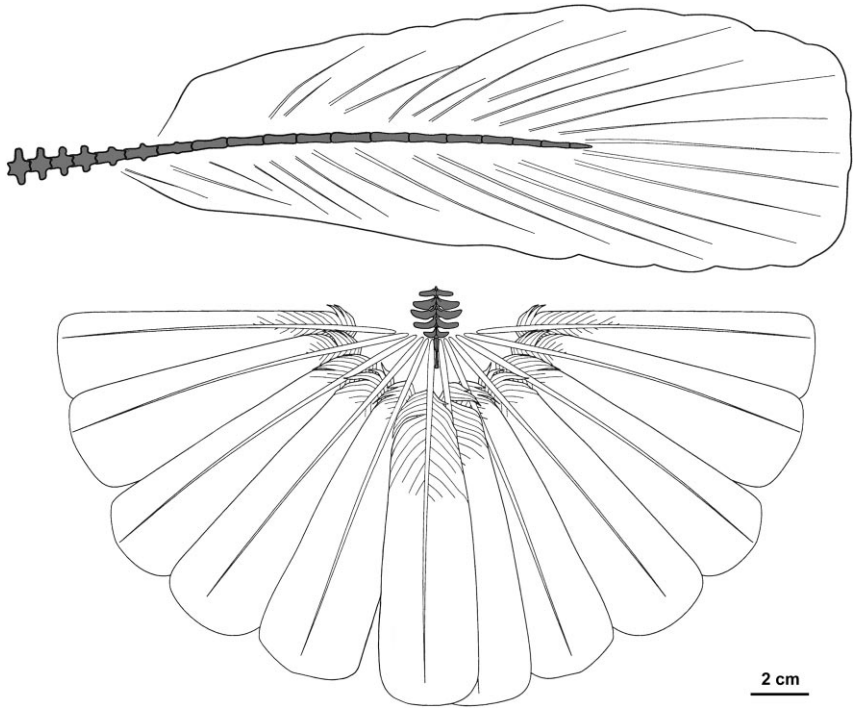
their presence cannot be confirmed in the ten known specimens of *Caudipteryx* (Z. Zhou 2001, personal communication). Maryanska et al.'s (2002) recent interpretation of oviraptorosaurs as birds still needs to be critically evaluated, but obvious problems of taxonomic sampling (e.g., no neornithine lineage included and *Archaeopteryx* and *Confuciusornis* were the only birds of the analysis) makes this phylogenetic inference dubious.

Overlooked by the supporters of an avian relationship for *Caudipteryx* is the fact that a great deal of homoplasy would have to be explained to nest this taxon within birds. For example, if Feduccia's (1999) interpretation of *Caudipteryx* as a flightless enantiornithine were correct, it would require the re-elongation of a bony tail, separation of the vertebral elements co-ossified into a pygostyle, development of new phalanges and finger re-elongation, substantial transformations in the sternum (from the single large and keeled element of Enantiornithes to the two small and separate plates of *Caudipteryx*), and loss of fusion of several compound bones (e.g., carpometacarpus, tibiotarsus, tarsometatarsus). The most parsimonious explanation, then, is that *Caudipteryx* is a non-avian theropod dinosaur with vaned feathers. The hypothesized homology between these feathers and those of extant birds has been explained by the developmental model of Prum (1999) that provides a framework for homologizing the various feather morphologies of non-avian theropods and for understanding the evolution of feather complexity. Further

support for the presence of vaned feathers among non-avian theropods has recently been provided by Norell et al. (2002), who described this type of feathers in an Early Cretaceous dromaeosaurid from China.

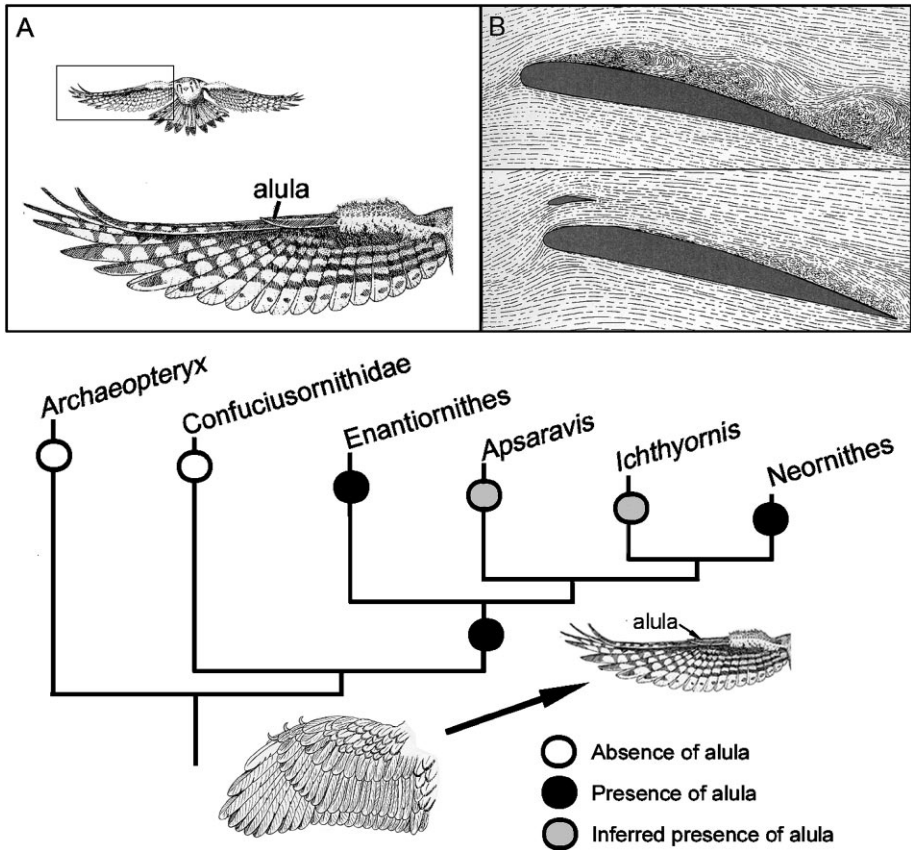
## Flight

Birds are characterized by their ability to move by active flapping flight, the functional and ecological contexts of which have been at the center of a long and heated debate (Hecht et al. 1985, Chatterjee 1997, Padian & Chiappe 1998, Feduccia 1999). Studies have demonstrated that aerodynamic features (e.g., elongated forelimb with flexible wrists, vaned feathers arranged in remiges and retrices, lateral orientation of shoulder socket) evolved prior to the origin of birds (Gauthier & Padian, 1985, Novas & Puerta 1997, Padian & Chiappe 1998, Sereno 1999). Over the course of bird evolution, the refinement of flight entailed the appearance of a complex suite of morphological specializations, which are understood within the context of phylogenetic relationship. Despite the fact that numerous other transformations (physiological, muscular, behavioral, neurological) must have been required to develop such a sophisticated locomotor system, each major lineage of Mesozoic birds provides direct evidence of the changes in the skeleton and plumage that led to the development of this system. *Archaeopteryx* had a wing without an alula (a feathered tuft attached to the first finger) that retained an ancestral configuration (humerus and hand longer than ulna-radius, first finger longer than metacarpals, complete set of manual phalanges) as well as a long bony tail supporting a frond-like array of feathers, a small and unkeeled sternum, a stout boomerang-shaped furcula (wishbone), and no evidence of postcranial pneumatization beyond the vertebral column. Although unquestionably interpreted as a flying bird (Hecht et al. 1985, Padian & Chiappe 1998, Burgers & Chiappe 1999, Feduccia 1999), the significantly smaller lift produced by its frond-like tail (Gatesy & Dial 1996) (Figure 11), the less developed flight musculature (Rayner 1991, 2001) inferred from the size and shape of its sternum, the apparent absence of a uniquely sophisticated and efficient air-sac respiratory system pneumatizing much of the skeleton, combined with the absence of a number of aerodynamic structures [e.g., alula (Sanz et al. 1996), spring-like U-shaped furcula (Jenkins et al. 1988)], suggests that *Archaeopteryx* was probably weaker and less maneuverable in flight compared to most of its extant relatives. The primitive wing of *Archaeopteryx* was essentially retained in the more derived confuciusornithids, but the long bony tail was shortened into a few free vertebrae and a stump, or pygostyle, formed by the fusion of the last vertebrae (Figure 8). The confuciusornithid wing had a propatagium, the skin fold joining the shoulder and wrist, a feature apparently unknown in *Archaeopteryx* and non-avian coelurosaurians (Clarke et al. 2001) that would have increased the area of the lift-generating airfoil. Estimates of important aerodynamic parameters such as wing loading also hint at refinements in the flight capabilities of these birds. Sanz et al. (2000) calculated the wing loading of *Confuciusornis* to be lower than that of *Archaeopteryx* and less than half that



**Figure 11** A scaled comparison between the frond-like tail of *Archaeopteryx* (top) and the fan-like tail of a pigeon (bottom) to illustrate the much larger airfoil attained by the latter design (after Gatesy & Dial 1996). Tail vertebrae in gray.

estimated for *Caudipteryx*. Although some confuciusornithid specimens preserve a pair of long tail feathers (Chiappe et al. 1999) (Figure 8), the aerodynamic function of their otherwise short-feathered tail would have been limited, in contrast to the tail fans typical of extant birds (Rayner 2001). The existence of a pair of long tail feathers in specimens of confuciusornithids (Chiappe et al. 1999) and enantiornithines (Zhang & Zhou 2000), however, provides evidence for elaborate feather differentiation as early as the Early Cretaceous, although it remains unclear whether this documents the evolution of marked sexual dimorphisms among these primitive birds (Chiappe et al. 1999). Many more features associated with the aerodynamic capabilities of living birds are recorded for the first time in Enantiornithes (Chiappe 1991, Sanz et al. 1996, Rayner 2001). These birds had modern wing configurations with the ulna-radius the longest segment, much shorter fingers (yet still clawed), and an alula (Figure 12). The alula plays an important aerodynamic role in controlling airflow over the dorsal surface of the wing during slow flight, thus enhancing maneuverability as well as performance during take-off and landing (Sanz et al. 1996). Although enantiornithines had large pygostyles that



**Figure 12** Aerodynamic function and phylogenetic distribution of the alula in birds. A small tuft of feathers attached to manual digit I (A), the alula functions by creating a slot along the leading edge of the wing. This slot (B, lower cross-section) decreases the turbulence originating on the dorsal wing surface at high angles of attack, thus enhancing control and maneuverability at low speeds, especially during take off and landing. The presence of an alula is considered a synapomorphy of Ornithothoraces (see Figure 4).

could have supported a feathered tail fan (Gatesy & Dial 1996, Rayner 2001), the available fossil material does not confirm this.

If an overall trend in size reduction is visible during the transition from non-avian coelurosaurians (e.g., dromaeosaurids, troodontids, oviraptorids) to basalmost birds (e.g., *Archaeopteryx*, *Rahonavis*), this pattern is further evidenced by the earliest enantiornithines, which were of sizes comparable to modern sparrows (e.g., *Iberomesornis*, *Sinornis*) and thrushes (e.g., *Concornis*, *Eoenantiornis*). General flight performance is often correlated with size reduction. Wing loading (for a given airfoil) decreases and power-to-weight ratio increases as body size decreases.

Furthermore, smaller birds are more maneuverable and flight is for them energetically less expensive. The advanced skeletal features of enantiornithines coupled with the presence of an alula and their small size suggest that even the earliest of these birds had aerodynamic abilities approaching those seen in extant forms.

A further step toward the modern flight condition is seen in the ornithurine *Apsaravis ukhaana*—that had a well-developed extensor process on the first metacarpal for the insertion of muscles involved in the automatic extension of the wing during upstroke-downstroke transition (Norell & Clarke 2001). This taxon along with more advanced flighted members of this clade [e.g., *Ichthyornis* (Marsh 1880, Clarke 2001), *Ambiortus* (Kurochkin 1985, 1999)] show the majority of the skeletal features associated with advanced flapping flight, suggesting that they had comparable abilities to those of extant birds.

## Growth and Development

Extant birds grow rapidly, and although their rates of growth vary depending on mode of development (altricial forms growing much faster than precocial ones), they normally reach adult size within a year. Although the bones of living birds are known to be fast-deposited and typically uninterrupted woven tissues (fibrolamellar bone), Mesozoic avians exhibited a great range of variation. The limb bones of *Rahonavis* (Chinsamy & Elzanowski 2001) and enantiornithines (Chinsamy et al. 1995) had thick cortices of slowly formed lamellar tissue (e.g., in *Rahonavis* 44% of the femoral wall was lamellar) that have multiple lines of arrested growth or LAGs, skeletal chronological indicators typically interpreted as representing annual pauses of postnatal bone deposition (Chinsamy et al. 1995, Ericson et al. 2001, Padian et al. 2001). Conversely, *Patagopteryx* (Chinsamy et al. 1995), *Hesperornis* (Houde 1987, Chinsamy et al. 1998), and *Ichthyornis* (Chinsamy et al. 1998) had bone walls formed primarily by fast growing fibrolamellar bone, with only *Patagopteryx* retaining a single LAG. The presence of LAGs in most non-neornithines suggests that in contrast to their living relatives, and perhaps all ornithurines, these basal birds may have required more than a year to reach adult size (Chinsamy et al. 1995, 1998; Chinsamy & Elzanowski 2001, Padian et al. 2001). This inference is consistent with known growth series where individuals lacking neonate features (fully fledged) are very differently sized, [e.g., in *Archaeopteryx lithographica* (Houck et al. 1990) and *Confuciusornis sanctus* (Chiappe et al. 1999), the smallest specimens are 50% and 60%, respectively, the size of the largest]. Histological evidence suggests that growth rates of basal birds were distinctly lower than those of their extant counterparts and that these elevated rates developed early in ornithurine history (Chinsamy et al. 1995, Padian et al. 2001, Chinsamy 2002).

Relatively rapid growth rates have been inferred in non-avian dinosaurs, which approached the condition seen in extant mammals and birds more than that of living non-avian reptiles (de Ricqlès 1980, Chinsamy 1990, 1993; Erickson et al.

2001; Padian et al. 2001). Histological data collected for basal birds indicates that their rates of growth were slower not only than those of extant birds but also those of their non-avian dinosaur relatives (Chinsamy & Elzanowski 2001, Padian et al. 2001). Causes underlying this evolutionary shift are not clear, but recent studies have proposed that this reduction in growth rates from non-avian dinosaurs to basal birds could have been achieved by shortening the duration of the rapid growth phase (i.e., deposition of fibrolamellar bone) that is characteristic of early ontogenetic stages in postnatal development (Padian et al. 2001, Chinsamy 2002). This shift could have led to the distinct decrease in size observed during the transition from non-avian theropods to enantiornithines (Padian et al. 2001) and has been used (Chinsamy & Elzanowski 2001) to support previous ideas (Elzanowski 1981) advocating superprecociality as the developmental strategy of enantiornithines and other basal birds. On the basis of the high degree of ossification seen in enantiornithine embryos, Elzanowski (1981) proposed a superprecocial developmental mode (independent young able to fly soon after hatching) for this group, because the skeletons of extant precocial hatchlings are significantly more ossified than those of altricial forms. A precocial developmental strategy for basal birds is supported by the distribution of this strategy among extant avian lineages (Chiappe 1995), where all the most basal taxa (e.g., paleognaths, galliforms, anseriforms) are characterized by having hatchlings that fall on the precocial side of the precocial-altricial spectrum. However, correlations between the extent of bone formation in fossil embryos and specific developmental strategies are weakly supported by embryogenetic studies of extant birds, which show that differences in the degree of ossification between superprecocial, precocial, and semiprecocial hatchlings are minor (Starck & Ricklefs 1998). Thus, although the shortening in the duration of the rapid growth phase could have been correlated to superprecociality and the development of precocial flight in basal, Mesozoic birds (Chinsamy & Elzanowski 2001), identifying this specific mode of development by recording degrees of ossification in fossil embryos is problematic. Interestingly, support for this proposal may come from the presence of fledged wings in some newly discovered enantiornithine juveniles (L. Chiappe, personal observations), suggesting the early onset of aerodynamic capabilities.

## DIVERSIFICATION AND EXTINCTION

### Basal Lineage Dynamics

Because of the incompleteness of the fossil record, lineage dynamics across time cannot be accurately observed simply from the temporal distribution of fossils. The oldest fossil representatives of a lineage provide evidence only for the minimal age of that particular taxon, but a more precise picture of the temporal pattern of lineage origination could emerge through calibration with a phylogenetic hypothesis. Definitive records of Enantiornithes (e.g., *Eoenantiornis*) and Confuciusornithidae are known from the 125-million-year-old Yixian Formation of China (see Swisher



et al. 2002 for radioisotopic dates). Enantiornithines (e.g., *Noguerornis* and an unnamed hatchling; Sanz et al. 1997, Chiappe & Lacasa-Ruiz 2002) may even be known from the apparently older lithographic limestones of Montsec (~130 mya) in Spain (Martín-Closas & López-Morón 1995). Even though the oldest ornithuromorphs (*Yixianornis* and *Yanornis*) come from deposits slightly younger than the Yixian Formation, calibration of our phylogeny (Figure 4) on the basis of the oldest records of confuciusornithids and enantiornithines implies that all these lineages must have diverged at least 130 million years ago. Indeed, it would not be surprising if early members of these lineages were to be found in Jurassic sediments in the future. The paucity of Jurassic deposits (e.g., less than 20% compared to the Cretaceous in the United States) (Clark et al. 2002), in particular those of continental origin (Benton 1994), may explain the fact that no bird of this age has yet been found with the exception of *Archaeopteryx*. The timing of divergences within Ornithuromorpha, however, is more controversial given the fragmentary nature of many specimens, in particular those closely related to extant birds (see below).

Although a wealth of new discoveries has shown that the Cretaceous was a time of active diversification for birds, this period has also proven to be one of widespread extinction. Indeed, no lineage of non-neornithine birds has ever been recorded in post-Mesozoic deposits (Figure 4). Feduccia (1995, 1999) has argued in favor of a dramatic extinction of all primitive Mesozoic lineages at the Cretaceous-Tertiary (K-T) boundary. Indeed, the last occurrence of enantiornithines (Chiappe 1993, Stidham & Hutchison 2001, Chiappe & Walker 2002) and other non-neornithine birds in strata very close to the K-T boundary (e.g., Lance and Hell Creek Formations of North America and Maastricht Formation of Europe) suggests that some primitive lineages may have become extinct along with larger dinosaurs in the terminal Cretaceous mass extinction (Stidham & Hutchison 2001). Nonetheless, the record of birds for the latest Maastrichtian (~67–65 mya) remains incomplete and the precise stratigraphic provenance of most specimens is not well documented. Further, most avian Late Cretaceous lineages are known by single occurrences (e.g., *Patagopteryx*, *Vorona*, *Apsaravis*) and of those known by ranges, some (e.g., ichthyornithiforms; Clarke 2002) have last occurrences in pre-Maastrichtian deposits, more than 10 million years before the K-T boundary. Thus, generalizations about a dramatic bottleneck in birds at the K-T boundary (Feduccia 1995, 1999), and the sudden eradication of all non-neornithine lineages, are not presently supported by the fossil record.

## Temporal Origin of Extant Lineages

A heated debate in current evolutionary biology involves the question of the timing of the origination of the extant lineages of birds. Estimates for the divergence of these neornithine birds based on the “clock-like” modeling of molecular sequence data predict that lineages (i.e., the extant traditional orders and families) originated deep in the Cretaceous (in some cases up to 90–100 million years ago; Hedges

et al. 1996, Cooper & Penny 1997, Kumar & Hedges 1998). However, the actual record of Cretaceous specimens that have been referred to extant lineages is sparse: Only a few of these are represented by more than an isolated element (e.g., *Ambiortus*, *Gansus*) (Table 3). This handful of fossils is either controversial, have not been studied in any detail, or their placement within Neornithes has been rejected. The incompleteness of most of the specimens referred as Cretaceous neornithines

**TABLE 3** Alleged records of Neornithes (modern birds) from the Mesozoic

Alleged taxonomy	Material	Formation and age
<b>NEORNITHES <i>incertae sedis</i></b>		
<i>Ceramornis major</i>	Coracoid	Lance Fm. (M)
<i>Gallornis straeleni</i>	Femur	Hateg Basin (M)
<b>PALAEOGNATHAE</b>		
<i>Ambiortus dementjevi</i>	Partial skeleton	Andaikhudag Fm. (Ha-Ba)
<b>NEOGNATHAE</b>		
<b>Galliformes</b>		
<i>Palintropus retusus</i>	Coracoids	Lance Fm. (M)
<b>Anseriformes</b>		
<i>Apatornis celer</i>	Synsacrum	Niobrara Fm. (Ca)
sp. Indet.	Partial skeleton	López de Bertodano Fm. (M)
sp. Indet.	Tarsometatarsus	Barun-Goyot Fm. (Ca)
<i>Anatalavis rex</i>	Humeri	Hornerstown Fm. (M*)
<b>Charadriiformes</b>		
sp. indet.	Coracoid	Lance Fm. (M)
<i>Cimoloperyx rara</i>	Coracoids	Lance Fm. (M)
<i>Cimoloperyx rara</i>	Carpometacarpus	Lance Fm. (M)
<i>Cimoloperyx maxima</i>	Coracoids	Lance Fm. (M)
<i>Graculavus velox</i>	Humerus	Hornerstown Fm. (M*)
<i>Graculavus velox?</i>	Carpometacarpus	Hornerstown Fm. (M*)
<i>Graculavus augustus</i>	Humerus	Lance Fm. (M)
<i>Telmatornis priscus</i>	Humerus	Hornerstown Fm. (M*)
	Carpometacarpus	Hornerstown Fm. (M*)
	Ulna	Hornerstown Fm. (M*)
<i>Laornis edwardsianus</i>	Tibiotarsus	Hornerstown Fm. (M*)
<i>Palaeotringa littoralis</i>	Tibiotarsus	Hornerstown Fm. (M*)
<i>Palaeotringa littoralis?</i>	Humerus	Hornerstown Fm. (M*)
<i>Palaeotringa vagans</i>	Tibiotarsus	Hornerstown Fm. (M*)
<b>Procellariiformes</b>		
<i>Lonchodystes estesi</i>	Tibiotarsus	Lance Fm. (M)
<i>Tyttostonyx glauciniticus</i>	Humerus	Hornerstown Fm. (M*)
sp. indet.	Furcula	Nemegt Fm. (Ca)

(Continued)

TABLE 3 (Continued)

Alleged taxonomy	Material	Formation and age
<b>Gaviiformes</b>		
" <i>Polarornis gregorii</i> " <sup>†</sup>	Partial skeleton	López de Bertodano Fm. (M)
<i>Neogaeornis wetzeli</i>	Tarsometatarsus	Quiriquina Fm. (M)
<b>Pelecaniformes</b>		
sp. indet.	Scapula	Nemegt Fm. (Ca)
<i>Elopteryx nopscai</i>	Femora	Hateg Basin Fm. (M)
<b>Psittaciformes</b>		
sp. indet.	Dentary	Lance Fm. (M)
<b>Gruiformes</b>		
<i>Horeznavis eocretacea</i>	Tibiotarsus	Khodzhakul Fm. (Al)

\*A Late Cretaceous age for the Hornerstown Formation of New Jersey is questionable; Olson (1994) discusses palynological evidence for the Palaeocene age of this deposit.

<sup>†</sup>*Polarornis gregorii* was only informally named and its Cretaceous age has been questioned (Clarke & Chiappe 2001).

Abbreviations: Al, Albian (112–97 mya); Ca, Campanian (83–74 mya); Ha-Ba, Hauterivian-Barremian (135–124.5 mya); M, Maastrichtian (74–65 mya). See Dyke (2001) for citations.

renders few characters useful for phylogenetic analyses (Clarke 1999, Dyke & Mayr 1999, Clarke & Chiappe 2001, Dyke 2001), and the poor understanding of the higher-level phylogenetic relationships of extant lineages further complicates their systematic consideration (Livezey & Zusi 2001). This scanty fossil record has, however, been used to hypothesize the existence of a number of extant lineages prior to the end of the Mesozoic (i.e., Pelecaniformes, Charadriiformes, Anseriformes, Gaviiformes, Galliformes, Psittaciformes) (Table 3), either by taking it at face value (Feduccia 1999) or by using it for the temporal calibration of morphological (Chiappe 1995) or molecular (Hedges et al. 1996, Cooper & Penny 1997) phylogenies. Nonetheless, it is imperative that existing Cretaceous reports of neornithine birds are treated with extreme caution (Clarke 1999, Dyke & Mayr 1999, Clarke & Chiappe 2001). Indeed, the earliest neornithine birds that are complete enough to be informative for cladistic analyses, and hence potentially informative for estimating the temporal divergence of extant lineages, come from rocks that are roughly 55 million years old (i.e., the Early Eocene Green River and London Clay formations of the United States and England, respectively; Dyke 2001), deposited some 10 million years after the end of the Cretaceous. Although a few specimens consisting of more than single bones do fill this temporal gap, they have not yet been considered within cladistic analyses. Certainly, it would not be surprising if future studies of these or even older specimens support their original placement within extant lineages, but such a work has yet to be undertaken. Although the presence of several immediate neornithine outgroups in the Late Cretaceous (e.g., *Ichthyornis*, *Limenavis*, *Apatornis*) does imply that the lineage leading to extant

birds must have differentiated prior to the end of the Mesozoic (Clarke & Chiappe 2001), this inference does not provide any information about the temporal divergence among extant lineages. To date, all Cretaceous specimens that have been submitted to rigorous cladistic analyses lay outside Neornithes (Clarke & Chiappe 2001). More well-preserved fossils and a better understanding of the relationships of modern clades are necessary to unravel the temporal divergence of extant avian lineages in pre-Tertiary times.

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