

## THE EARLY EVOLUTIONARY HISTORY OF BIRDS

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**Abstract:** With more than 10,000 species – roughly twice as many as there are mammals or lizards – birds are by far the most diverse group of living land vertebrates. However, this enormous diversity is just a remnant of an ancient evolutionary radiation that can be traced back to the Jurassic, to the 150 million-year-old *Archaeopteryx* from southern Germany. Research on the early history of birds and the development of flight has been at the forefront of paleontology since the advent of evolutionary thought. For most of this time, however, the available evidence was limited to a small number of fossils largely restricted to near-shore and marine environments, and greatly separated both anatomically and in time. A burst of discoveries of Cretaceous birds over the last two decades has revealed a hitherto unexpected diversity; since the early 1990s, the number of new species described has more than tripled those known for much of the last two centuries. This rapid increase in discoveries has not only filled much of the anatomical and temporal gaps that existed previously, but has also made the study of early birds one of the most dynamic fields of vertebrate paleontology.

**Key words:** Evolution, Mesozoic, birds

### A CENTURY OF CONTROVERSY: THE ORIGIN OF BIRDS

Historical proposals for the ancestry of birds have included almost every group of reptiles (Witmer, 1991, 2002; Padian and Chiappe, 1998; Chiappe, 2001). Today, alternatives to the widely accepted view that birds evolved from theropod dinosaurs (Chatterjee, 1997; Chiappe, 2001; Gauthier and Gall, 2001) include poorly sustained hypotheses identifying a variety of primitive archosauromorphs (Tarsitano and Hecht, 1980; Feduccia and Wild, 1993; Welman, 1995) or crocodylomorphs (Martin, 1983; Martin *et al.*, 1980; Martin and Stewart, 1999) as the closest relatives of birds.

The notion that the ancestry of birds is to be found among primitive archosauromorphs can be traced to the discovery of *Euparkeria* from the Early Triassic of South Africa (Broom, 1913). Nonetheless, it was Heilmann (1926) in his influential book *The Origin of Birds*, who championed this idea. At the time, discussions about the origin of birds were influenced by the ‘Law of Irreversibility’ – namely, that structures once lost cannot re-evolve. Although noticing a great deal of similarity between birds and theropods, Heilmann (1926) embraced this idea of archosauromorph ancestry (in the shape of an animal such as *Euparkeria*) because these reptiles lack the specializations seen in theropod dinosaurs. Central to his argument was the apparent loss of clavicles in theropods – an observation at odds with the evolutionary view of structural irreversibility that prevailed at the time (Padian and Chiappe, 1998). Despite the subsequent discovery of clavicles in a variety of theropods (e.g., Camp, 1936; Chure and Madsen, 1996; Makovicky and Currie, 1998), this ‘default’ archosauromorph hypothesis remained virtually unchallenged until the early 1970s. Using primarily similarities in the braincase, Walker (1972) argued for a close relationship between birds and basal crocodylomorphs (e.g., sphenosuchians). Almost at the same time, Ostrom (1973) resurrected the 19th Century notion of a theropod ancestry for birds (Witmer, 1991, 2002; Padian and Chiappe, 1998). The work of Walker and Ostrom provided new impetus for the re-examination of the origin of birds, with the emergence of the crocodylomorph and theropod hypotheses as a possible alternative to the archosauromorph ideas that had prevailed for much of the 20th Century. Extending Walker’s work, Martin *et al.* (1980; see also Martin and Stewart, 1999) regarded similarities in

the structure of the teeth and ankle as evidence for a close relationship between birds and extant crocodiles, whereas Welman (1995) considers the braincase of *Euparkeria* as indicative of an avian relationship. While both the archosauromorph and crocodylomorph hypotheses highlighted similarities with birds, many of them have either been questioned or have subsequently been discovered in dinosaurs. If one were to entertain either of these hypotheses they would have to go further to explain the vast number of similarities that support a close relationship between birds and theropod dinosaurs (Chiappe and Dyke, 2002).

Since Ostrom's pioneering studies (1973, 1976), a wealth of evidence including similarities in the skeletal, egg structure, nesting behavior, integument, and bone microstructure has been accumulated in support of the hypothesis that birds originated within small and predominantly terrestrial theropods (Gauthier, 1986; Chiappe, 2001, 2004; Holtz, 2001; Norell *et al.*, 2001; Padian *et al.*, 2001; Chiappe and Dyke, 2002; Clark *et al.*, 2002; Xu *et al.*, 2003). Alternative hypotheses, however, compete regarding the closest theropod group to birds, with dromaeosaurids, troodontids, oviraptorids, and alvarezsaurids among the most commonly cited (e.g., Gauthier, 1986; Perle *et al.*, 1993; Sereno, 1999; Chiappe *et al.*, 1998; Elzanowski, 1999; Xu *et al.*, 2000; Holtz, 2001; Norell *et al.*, 2001; Clark *et al.*, 2002).

## UNEXPECTED DIVERSITY: THE MESOZOIC AVIFAUNA

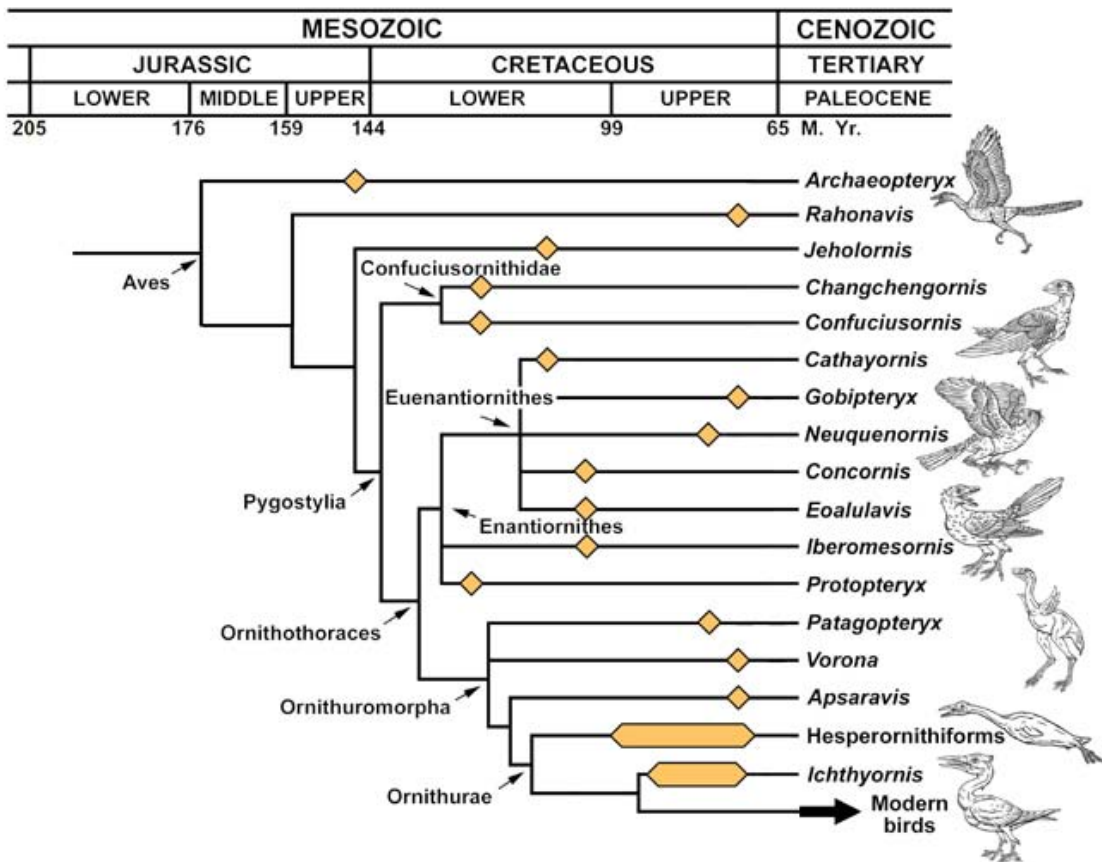
For almost a century, knowledge of the Mesozoic avifauna was greatly limited to just the Late Jurassic *Archaeopteryx* and a series of fossils from the Late Cretaceous Pierre Seaway of North America. The anatomy of these Late Cretaceous birds (e.g., *Hesperornis* and *Ichthyornis*) testified to an enormous gap in the early history of the group when compared to the older and much more primitive *Archaeopteryx*. Discoveries of recent years have considerably filled this gap (Chiappe and Dyke, 2002; Chiappe and Witmer, 2002) and a genealogical framework for much of the diversity of Mesozoic birds has emerged (Fig. 1).

### ISLAND DWELLERS: *ARCHAEOPTERYX* AND *RAHONAVIS*

Although ten skeletal specimens and a feather (Elzanowski, 2002; Mayr *et al.*, 2005) of *Archaeopteryx* have been found in lagoonal limestones of a tropical archipelago – deposits today clustered in central Bavaria, Germany – some of these have been used to erect new species, albeit not very convincingly. A single, mostly disarticulated specimen of *Rahonavis* is known from the Late Cretaceous of Madagascar (Forster *et al.*, 1998), when the island had already lost its connections with both Africa and India. Although they lived some 75 million years apart, these island dwellers are the most anatomically primitive known birds, having long bony tails, primitive proportions in the pelvis, and incomplete fusion of some compound bones (e.g., tarsometatarsus, tibiotarsus) (Fig. 2).

If the single species approach is adopted, then the ten skeletal specimens of *Archaeopteryx* ranged in size between a jay and a small gull – although size comparisons of this bony-tailed bird with living species remain approximate. In spite of the spectacular preservation of several specimens (Hecht *et al.*, 1985; Mayr *et al.*, 2005), limited anatomical information is available for certain areas of the skeleton; indeed not all specimens preserve the same details.

The anatomy of *Archaeopteryx* illustrates the most primitive condition seen in birds (Fig. 2), one that in many respects only narrowly departs from nonavian theropods. Although its toothed skull was more triangular, it shows a great deal of similarity to the latter (e.g., interdental plates, hooked ectopterygoid, quadrate anatomy) (Elzanowski, 2002; Mayr *et al.*, 2005). The sternum of *Archaeopteryx* was apparently small and cartilaginous (the bone identified by Wellnhofer (1993) as a sternum has been proved to be the



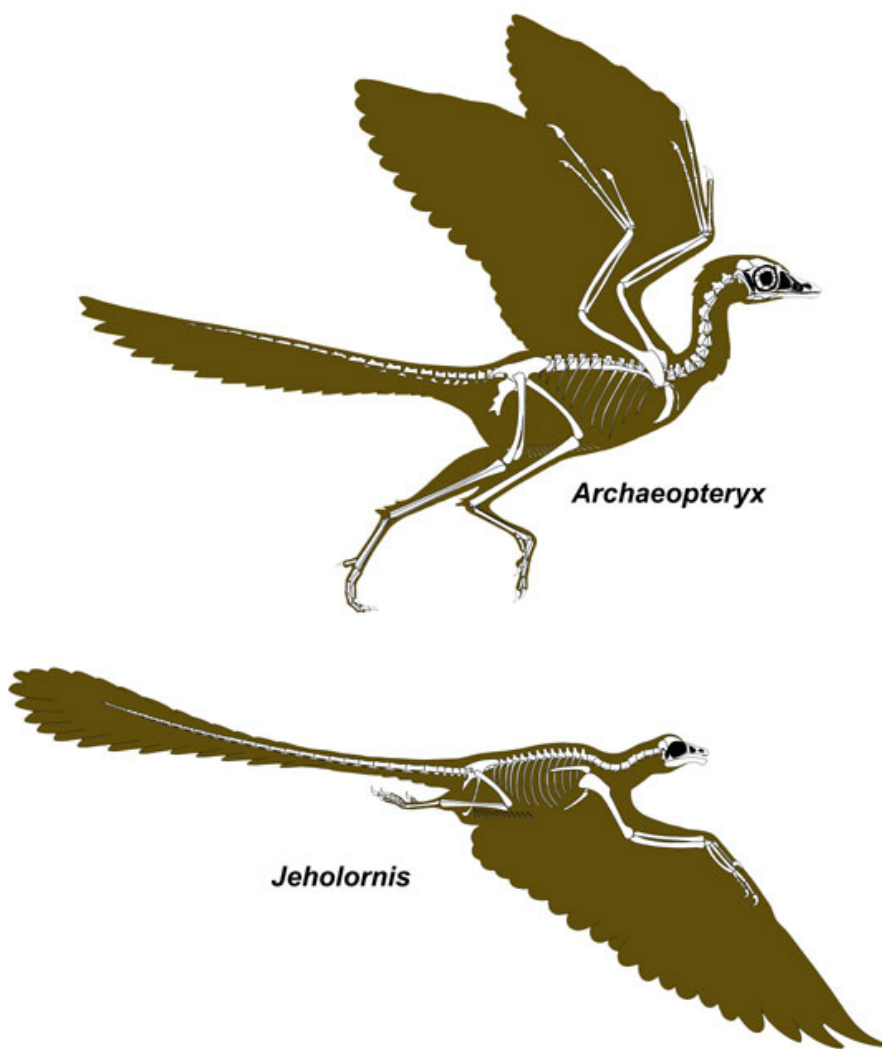
**Fig. 1.** Phylogenetic relationships and temporal occurrences of the major lineages of Mesozoic birds.

coracoid) and linked to the pelvis by a basket of belly ribs (gastralia) similar in number (12-13 pairs) and appearance to those of nonavian theropods (Norell and Makovicky, 1997). Its long trunk lacked the rigidity of extant birds and its shoulder girdle did not have many of their specializations (e.g., strut-like coracoid, triosseal canal) for flight. Despite a striking similarity in the shape and number of feathers (11-12 primaries and 12-14 secondaries; Elzanowski, 2002) to living birds, just like in nonavian theropods the forelimb of *Archaeopteryx* terminated with a long, powerfully clawed hand. Indeed, the shape and proportions of the pelvic bones and hindlimb are equally primitive. Shorter than most nonavian theropods (21-22 elements; Elzanowski, 2002), the frond-like, feathered tail of *Archaeopteryx* retained the long prezygapophyses (anterior zygapophysial articulations) as well as other details seen in these dinosaurs. As in most nonavian theropods, and all birds, the skeleton of *Archaeopteryx* was lightweight and pneumatized – in particular, the vertebrae and furcula (wishbone) were invaded by air sacs (Britt *et al.*, 1998; Christiansen and Bonde, 2000).

The anatomy of *Rahonavis* also suggests that this bird was a lightweight predator (Forster *et al.*, 1998), with a wingspan comparable to that of a red-tailed hawk. Quill knobs preserved on its forelimb indicates at least 10 flight feathers attached to the ulna, a number within the range seen in living birds. The structure of the shoulder girdle – in particular, the presence of a mobile glenoid – approaches more that of extant birds than does the rigid, fused girdle of *Archaeopteryx* and some other early birds (e.g., confuciusornithids). The reconstructed position of the scapula with respect to the rib cage suggests *Rahonavis*

was able to flap its wings with greater amplitude than *Archaeopteryx* or nonavian theropods (Forster *et al.*, 1998). All these features are consistent with well-developed aerodynamic capabilities. However, perhaps the most striking anatomical feature of *Rahonavis* is the presence of an enlarged, sickle-shaped foot claw, presumably used for slashing prey, a specialization typical of dromaeosaurid and troodontid theropods – a proportionally smaller version of this condition has also been identified in *Archaeopteryx* (Mayr *et al.*, 2005).

Because of this apparently mosaic combination of features, some have claimed *Rahonavis* to in fact be composed of the forequarters of a bird mixed with the hindquarters of a nonavian theropod (Geist and Feduccia, 2000). The preservation of the fossil material as well as carefully conducted analyses by its describers indicates otherwise (Chiappe and Dyke, 2002). Nonetheless, the precise evolutionary relationships of *Rahonavis* remain unclear. Forster *et al.* (1998) regarded it as closer to *Archaeopteryx* than to other birds, although cautioning about the possibility of *Rahonavis* being more akin to extant birds (see



**Fig. 2.** Skeletal reconstructions of the Late Jurassic *Archaeopteryx* and the Early Cretaceous *Jeholornis*. Drawings not to scale.

also Chiappe, 2002a; Fig. 2). Although subsequent studies have also supported a basal placement for *Rahonavis* within birds (Holtz, 1998; Chiappe, 2002a; Zhou and Zhang, 2002a), some workers (Holtz, 2001; Clark *et al.*, 2002; Makovicky *et al.*, 2005) have also hypothesized that this fossil in fact falls immediately outside the group.

Although there is little doubt that *Archaeopteryx* was able to fly (Hecht *et al.* 1985; Padian and Chiappe 1998; Feduccia 1999), the limited lift produced by its frond-like tail, the presumably weak flight musculature as inferred from the absence of a bony sternum, the lack of an alula and several other important aerodynamic structures suggests that *Archaeopteryx* was most likely a weaker and less maneuverable flier than most of its living relatives – the Solnhofen bird probably required of a take-off run to become airborne (Burgers and Chiappe, 1999). Similar aerodynamic inferences can be made for *Rahonavis* and other long-tailed birds.

### A LACUSTRINE CORNUCOPIA: THE NEW DIVERSITY FROM CHINA

If there is one region that has dramatically contributed to our understanding of the origin and early evolution of birds, this is the northeastern Liaoning Province of China (Zhou *et al.*, 2003). The exquisite and numerous fossils recovered from these and other Early Cretaceous localities in China include more than a dozen species breaching the enormous evolutionary gap between *Archaeopteryx* and modern birds (Fig. 1). The majority of these birds are temporally distributed between two lacustrine beds in Liaoning: the approximately 128-121 million-year-old Yixian Formation (Swisher *et al.*, 2002; Zhou *et al.*, 2003) and the slightly younger Jiufotang Formation (approximately 120 million years old; He *et al.*, 2004).

The turkey sized *Jeholornis* (Zhou and Zhang, 2002a) from the Jiufotang Formation also illustrates the primitive, long-tailed condition of *Archaeopteryx* and *Rahonavis* (Fig. 2). This bird is one of the largest from prior to the Late Cretaceous. The skull is triangular, with deep and robust jaws. Only a few tiny teeth are present towards the tip of the lower jaw and these are absent in the upper jaw (Zhou and Zhang, 2003a). Like in *Rahonavis*, the shoulder girdle articulation is mobile. *Jeholornis*, however, shows significant modifications with respect to *Archaeopteryx*. The coracoid is elongate and the curved scapula tapers distally, thus approaching the condition seen in extant birds (Zhou and Zhang, 2002a). The sternum of *Jeholornis* is ossified and large. The forelimb of this bird is also longer relative to its hindlimb than that of *Archaeopteryx*. Its powerfully clawed hand is almost as long as the humerus, proportionally shorter than that of *Archaeopteryx*, beginning the evolutionary transition towards living birds where the proximal portion of the forelimb is substantially longer than its distal counterpart. The pelvis is similar to that of *Archaeopteryx* and *Rahonavis* the pubis is vertically oriented although the portion at which the two counterparts are joined to one another (i.e., the pubic apron) is shorter than that of at least the former. As in most birds the foot had a retroverted first toe (hallux). Yet, the hindlimb exhibits several features ancestral to all birds, including incompletely formed compound bones (e.g., tibiotarsus, tarsometatarsus), the presence of a splint-like fifth metatarsal, and a very short hallux (Zhou and Zhang, 2002a, 2003a). Furthermore, the tail of this animal is longer than that of any other bird. Even though its initial report described approximately 22 caudals (Zhou and Zhang, 2002a), two recent specimens have shown that its tail contains 27 vertebrae (Zhou and Zhang, 2003a) – several more elements than the shorter tail of *Archaeopteryx* – and that a fan-shaped tuft of feathers attached to its distal end. These new specimens have also documented the presence of long and asymmetrically vaned feathers on the forelimbs. Zhou and Zhang's study (2002a) was unable to precise whether *Jeholornis* was closer to extant birds than *Rahonavis* – their cladogram placed these two long-tailed birds in a trichotomy with all other birds except *Archaeopteryx*. The discovery that *Jeholornis* had a tail longer than that of *Archaeopteryx* may add more to this conflict, especially when the tail of *Rahonavis* is incompletely known. Nonetheless, these three birds are undoubtedly more primitive than any other one.

In the same month as the initial report of *Jeholornis*, another Jiufotang bird with long asymmetrical flight feathers and a long tufted tail, *Shenzhouraptor*, was reported by Ji *et al.* (2002). In addition to being three quarters the size of the holotype of *Jeholornis*, Ji *et al.* (2002) reported a few other differences including the lack of teeth and a greater number of caudals. As indicated earlier, however, this latter difference has been shown to be null by new fossils documenting that the tail of the holotype of *Jeholornis* is missing several proximal caudals (Zhou and Zhang, 2003a). Unfortunately, Zhou and Zhang (2003a) made no comparisons between *Jeholornis* and *Shenzhouraptor*, but we believe that the "absence" of teeth in the latter may well be a preservational artifact. Differences notwithstanding, we believe that the great similarity between *Jeholornis* and *Shenzhouraptor* seriously raises the possibility that these birds are the same species. Very similar to these birds is *Dalianraptor*, also known from the Jiufotang Formation (Gao and Liu, 2005). However, several differences in the morphology and proportions of the forelimb (e.g., much shorter forelimbs, longer digit I) suggest that *Dalianraptor* is neither *Jeholornis* nor *Shenzhouraptor*, although it is likely a close relative of these birds.

From the same Jiufotang beds as *Jeholornis*, *Shenzhouraptor*, and *Dalianraptor* comes a great diversity of short-tailed birds with opisthopubic pelves, whose genealogically are closer to extant avians than the long-tailed forms. Perhaps the most primitive short-tailed bird is *Sapeornis* (Zhou and Zhang, 2002b, 2003b), a large animal with a wingspan comparable to that of a turkey vulture (Fig. 3). At least half-a-dozen specimens of this unusual bird have been found. *Sapeornis* has a relatively short skull with conical and robust teeth restricted to the tip of the rostrum, and lacking them in its lower jaws. The temporal region of the skull remains largely unmodified, with at least a complete upper temporal fenestra. In the shoulder girdle, the articulation of the scapula and the coracoid is mobile but the latter bone is short and axe-shaped. Interestingly, no specimen so far preserves an ossified sternum. This last fact suggests that the sternum could have been cartilaginous and that the flight muscles needed to power the long wings of this bird could have been originated on the expanded distal coracoids. The furcula is very robust and shaped like a boomerang, with an angle of more than 100 degrees between its branches having a short hypocleideum – the most primitive known occurrence of this feature within bird evolution. The elongate forelimb of *Sapeornis* is much longer than that of *Archaeopteryx*, *Jeholornis*, and *Shenzhouraptor*, reaching approximately 1.5 times the length of the hindlimb. The humerus is shorter than the ulna-radius and pierced by a large proximal foramen of uncertain function. The hand is about the same length as the humerus, as in the Chinese long-tailed birds, but the presence of a clawless, reduced third digit illustrates the first stage of finger reduction characterizing early bird evolution. Like in *Archaeopteryx* and other long-tailed birds, the pelvis remains unfused but its pubic symphysis has become shorter. A full basket of gastralia fills the space in front of the pelvis in several specimens. Perhaps the most notable difference when compared to its more primitive long-tailed relatives is the abbreviation of the bony tail, which was limited to a rather short pygostyle following 6-7 free caudals (Fig. 3). Based on the information of the holotype alone, Zhou and Zhang (2002b) suggested that *Sapeornis* is the most primitive short-tailed bird. This interpretation, however, needs to be tested in light of subsequent better preserved specimens and detailed comparisons with primitive short-tailed birds such as *Confuciusornis*.

By far the most abundant bird from the Mesozoic of China (and the world) is the toothless *Confuciusornis* (Hou *et al.*, 1995; Chiappe *et al.*, 1999) (Fig. 3), a short-tailed species that maybe only slightly more derived than *Sapeornis* (Zhou and Zhang, 2002b). Hundreds of well-preserved specimens of this bird have been collected from both the Yixian and Jiufotang formations (Zhou *et al.*, 2003). The size of these fossils falls within a wide spectrum but the average specimen has dimensions comparable to those of a magpie. Although several species of *Confuciusornis* have been named, most published specimens seem to comprise a single one (i.e., *C. sanctus* see Chiappe *et al.*, 1999), thus providing the best sample for studying intraspecific variation in any Mesozoic bird. Very similar to *Confuciusornis* is the

equally toothless *Changchengornis*, a bird known from a single specimen of the Yixian Formation (Ji *et al.*, 1998; Chiappe *et al.*, 1999) and differing from *Confuciusornis* by its strongly curved beak and a few other skeletal details.

Confuciusornithids are very primitive in many respects. In the first place, the skull of *Confuciusornis* (and likely of *Changchengornis*) is remarkable in exhibiting a complete diapsid (upper and lower) temporal fenestrae (Chiappe *et al.*, 1999)—a design that would have greatly limited cranial kinesis. The shoulder bones of these birds are fused into a rigid scapulocoracoid, a condition more primitive than that of the long-tailed *Rahonavis*, *Jeholornis*, and *Sapeornis*. The forelimb is proportionally much shorter than in the latter birds, approaching the length of the hindlimb as in *Archaeopteryx*. The forelimb bones also retain primitive proportions—the hand is the longest segment and the ulna-radius is shorter than the humerus. The robust wishbone has the boomerang appearance of *Archaeopteryx* and the sternum is es-



**Fig. 3.** Skeletal reconstructions of the Early Cretaceous *Confuciusornis* and *Sapeornis*. Drawings not to scale.

entially flat (although some specimens do have a faint caudal ridge), lacking the prominent ventral keel that is seen in more advanced birds. Like apparently all basal avians, confuciusornithids had a full set of gastralia, although with fewer rows than seen in *Archaeopteryx*. The hindlimbs are robust and the reversed hallux is half (*Confuciusornis*) to two-thirds (*Changchengornis*) the length of the second toe. The plumage of these Chinese birds is beautifully preserved – both taxa of confuciusornithids display a pair of long, ribbon-like tail feathers that extend more than half the length of their skeletons. In *Confuciusornis*, of which many well-preserved specimens are known, these feathers are either present or absent, a pattern often interpreted as the result of sexual dimorphism. This argument, however, has yet to be sustained on the basis of morphometric analyses of bones, including specimens with and without these feathers (Chiappe *et al.*, 1999).

By far the most speciose group of Early Cretaceous birds from China – indeed the rest of the Mesozoic record – were members of Enantiornithes (Chiappe and Walker, 2002) (Fig. 4). Close to one-third of the 25 or so valid species of these birds are from continental Chinese deposits, and mostly from Liaoning. The remaining diversity of this lineage has been recorded from rocks spanning nearly the whole Cretaceous and from every continent except Antarctica. Although most often recorded from inland deposits, enantiornithines are also known to have inhabited coastal and marine environments, and their range even extended into polar regions (Chiappe, 1996). The oldest known enantiornithine is possibly the Chinese *Protopteryx* (Zhang and Zhou, 2000), which comes from Early Cretaceous rocks of Hebei Province (Dabeigou Formation) that appear to be slightly older than those of Liaoning's Yixian Formation.

Early Cretaceous enantiornithines are represented by small toothed species such the Chinese *Protopteryx* (Zhang and Zhou, 2000, *Eoenantiornis* (Hou *et al.*, 1999), and *Longipteryx* (Zhang *et al.*, 2001) (Fig. 4), and the Spanish *Concornis* (Sanz *et al.*, 1995) and *Eoalulavis* (Sanz *et al.*, 1996). If an overall trend in size reduction is visible during the transition from nonavian maniraptoran (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 and

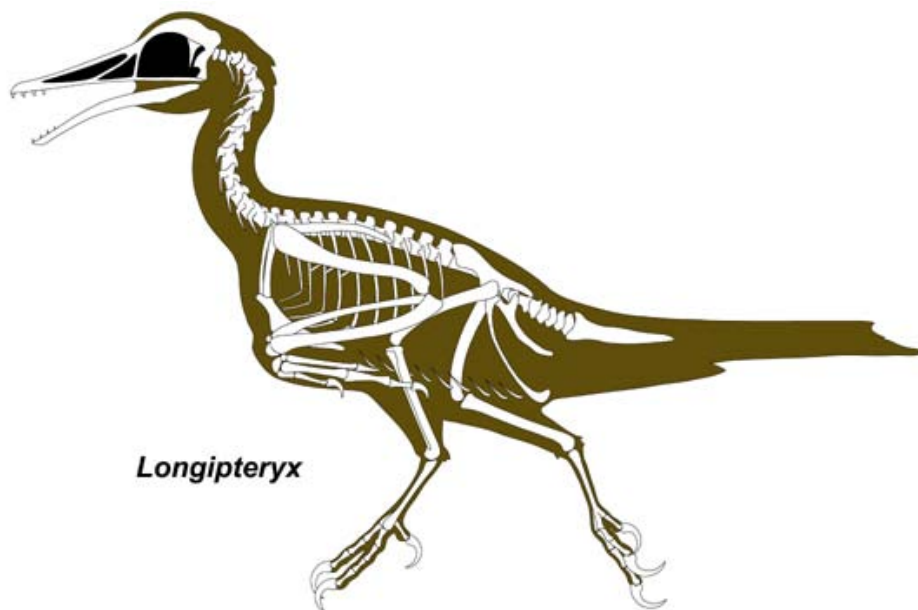


Fig. 4. Skeletal reconstructions of the Early Cretaceous enantiornithine *Longipteryx*.



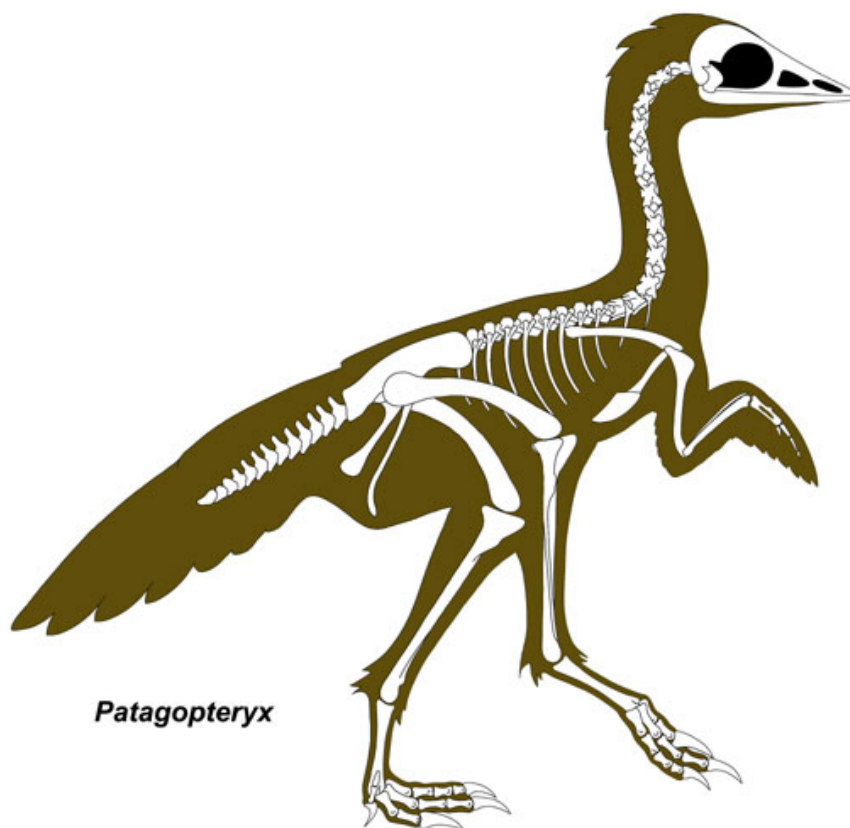
thrushes. General flight performance is often correlated with size reduction and the overall anatomy of the flight apparatus of enantiornithines shows similarities to those of living birds in wing proportions, the large size of the sternum, a Y-shaped furcula, and an alula – the latter structure, a small tuft of feathers attached to the first finger of the hand, plays a critical role in controlling take-off and landing (Sanz *et al.*, 1996). All these features suggest that even the earliest enantiornithines possessed a much more sophisticated flying apparatus than that of their avian predecessors – enantiornithines were likely able to take-off from a stand still. 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 (Chiappe and Calvo, 1994; Chiappe, 1995; Martin, 1995; Zhou, 1995; Sanz *et al.*, 1995; Sereno *et al.*, 2002). A distinct increase in size characterizes later enantiornithine evolution – in the Late Cretaceous, the Mongolian *Gobipteryx* (Chiappe *et al.*, 2001), the only toothless enantiornithine, reached the size of a quail, and the Argentine *Enantiornis* (Walker, 1981; Chiappe, 1996) had a wing span of nearly one meter.

In addition to rich accumulations of more basal avians, the Early Cretaceous deposits of China have also provided critical information for understanding the evolution of birds much more closely related to those of today.

### **BASAL ORNITHUROMORPHS: THE PRIMITIVE FORERUNNERS OF MODERN AVIANS**

For nearly the entire history of paleornithology, the evolutionary transformations leading to the origin of modern birds (i.e., Neornithes) were established on the evidence mostly provided by two lineages of seabirds, the specialized diving hesperornithiforms and the less well-known *Ichthyornis* (Marsh, 1880). Developments over the last decade, however, have furnished us with many more Mesozoic players from which to examine this important evolutionary event. Alongside hesperornithiforms and *Ichthyornis*, this new diversity constitutes the Ornithuromorpha, a vast clade sharing a common ancestor with Enantiornithes and containing all 10,000 species of living birds (Fig. 1). Despite these new discoveries, the precise genealogical relationships of most Mesozoic ornithuromorphs are not entirely clear.

Among the best known of these taxa is the flightless *Patagopteryx* from the Late Cretaceous (early to middle Campanian) of northwestern Patagonia (Argentina) (Chiappe, 2002b) (Fig. 5). Known from several specimens, this hen-sized bird is one of the most primitive known ornithuromorphs and the best-represented bird from the Mesozoic of the Southern Hemisphere. Its skull is incompletely known and it is thus uncertain whether it was toothed. The cranial anatomy of this bird, however, shows a significant departure from that of more primitive forms, evidenced by the complete reduction of the postorbital and the incorporation of the squamosal into the braincase. An important functional corollary of this transformation is the disappearance of individualized temporal openings, a landmark in the evolution of the modern avian skull. However, several cranial features (e.g., quadratopterygoid fusion, interlocked quadratosquamosal articulation) suggest that the kinematic capabilities also characteristic of the modern avian skull were not yet developed in *Patagopteryx* (Chiappe, 2002b). The cervical vertebrae of *Patagopteryx* have the saddle-shaped articulations (i.e., heterocoely) typical of modern avians – although a tendency towards this specialized type of vertebral articulation can be seen in Enantiornithes, *Patagopteryx* is the most primitive bird with fully heterocoelous vertebrae and most likely, the tri-partite functional subdivision typical of the neck of modern birds. With a long trunk and a relatively small (nine) number of synsacral vertebrae, *Patagopteryx* represents an early stage in the elongation of the neck and sacral region seen in more advanced ornithuromorphs. Its simplified shoulder, apparently reduced furcula and sternal keel, and strongly abbreviated forelimbs suggest that it was flightless, albeit a specialization clearly evolved from flying ancestors (Chiappe, 2002b) (Fig. 5). Several other advanced features can be seen in its robust pelvis. Paramount are the lack of a pubic symphysis and the proximocaudal



**Fig. 5.** Skeletal reconstructions of the Late Cretaceous basal ornithuromorph *Patagopteryx*.

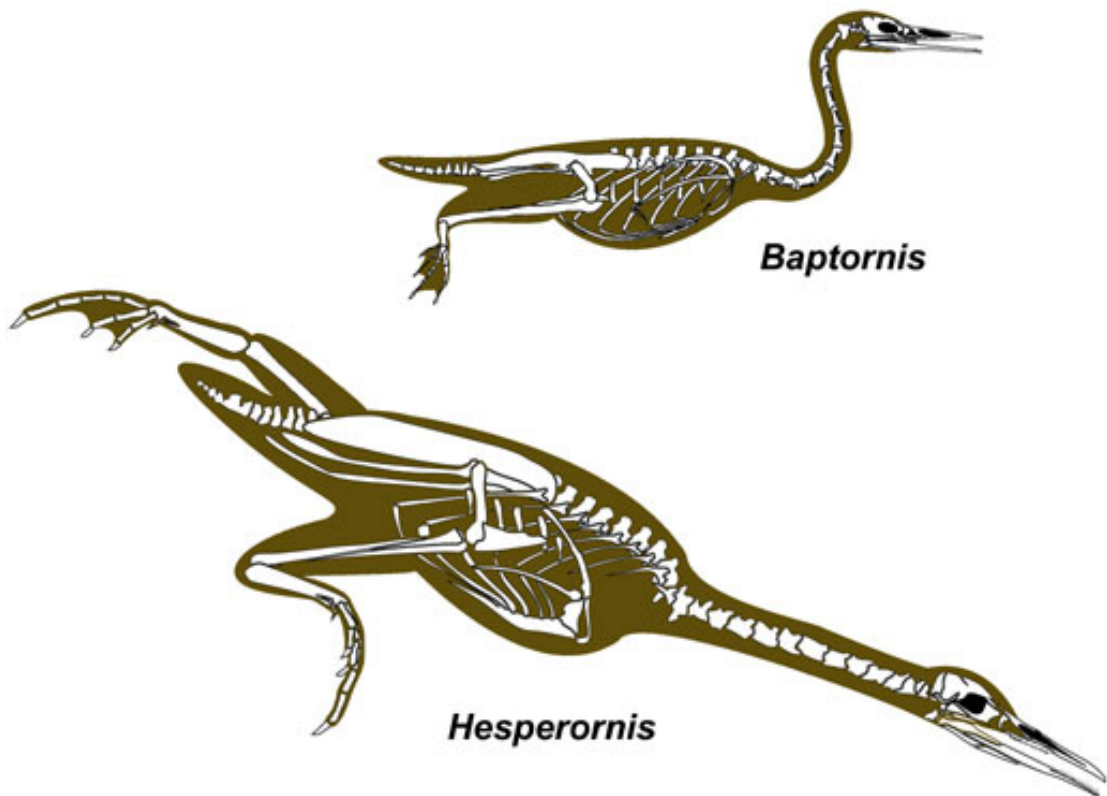
process of the ischium, which primitive conditions are widespread among more basal birds. The robust and muscular hindlimb of this obligated ground-dweller is more than twice as long as the forelimb; the short tarsometatarsus and long toes suggests *Patagopteryx* was a slow moving bird.

A number of other basal ornithuromorphs have recently been discovered that are many millions of years older than *Patagopteryx*. These discoveries include two exceptionally well preserved toothed birds from the Early Cretaceous of China, the equal-sized *Yanornis* and *Yixianornis* (Zhou and Zhang, 2001; Zhou *et al.*, 2002) from the Jiufotang Formation and the older and much smaller *Hongshanornis* (Zhou and Zhang, 2005) from the Yixian Formation. Although the precise genealogical relationships of these taxa currently remain unclear, the presence of a pubic symphysis suggests that these taxa may be more primitive than *Patagopteryx*. These birds also retain a number of more primitive avian characteristics (i.e., gastralia, long fingers that retain claws) while at the same time having an essentially modern flight apparatus. The pectoral girdle of both *Yanornis* and its shorter-snouted contemporary *Yixianornis* closely approach the condition seen in living birds (i.e., coracoid with a wide base and rounded procoracoid, curved scapula) – both these taxa were clearly capable of well-controlled and active flapping flight and future studies of them are likely to clarify further aspects of the anatomical transition towards living birds.

Both *Patagopteryx* and these Chinese taxa appear to be more primitive than another recently discovered basal ornithuromorph, the Mongolian Late Cretaceous *Apsaravis* (Norell and Clarke, 2001; Clarke and Norell, 2002). The single known specimen of *Apsaravis* consists of a well-preserved skeleton lacking most of the skull together with portions of the forelimbs and feet. Its lower jaw is devoid of

teeth and it is possible that *Apsaravis* was the most primitive toothless ornithuromorph (although *Hongshanornis* has been regarded as toothless (Zhou and Zhang, 2005), the poor preservation of the only known specimen makes it difficult to determine whether it truly lacked teeth). Many features of the anatomy of *Apsaravis* show clear similarity to modern avians (e.g., short fused dentary symphysis, reduced number of trunk vertebrae). Among the most notable is the development of a broad pelvis in which the pubis and ischium are widely separated from each other. Another important transformation of functional significance has to do with metacarpal I developing a pronounced extensor process. In extant birds, this feature is involved in the automatic extension of the hand by the propatagial ligaments (Vazquez 1994). The appearance of a pronounced extensor process in the carpometacarpus of *Apsaravis* indicates that this bird was able to extend its wing automatically (Clarke and Norell, 2002), a functional property that highlights the sophistication reached by the flight apparatus of this and more advanced ornithuromorphs.

Even more closely related to modern birds, although representing an early example of flightlessness, are the diving hesperornithiforms (Fig. 6). Despite having been known since the 19th century and in some instances monographed (i.e., *Hesperornis regalis* Marsh 1880), much revisionary work on their anatomical diversity and genealogical interrelationships remains to be done. Ranging greatly in size – the largest being comparable to that of an Emperor Penguin – these birds are characterized by having an elongate skull with a sharp and toothed snout, minute forelimbs, a long neck and short trunk, and a robust hindlimb specialized for aquatic locomotion (Marsh, 1880; Martin and Tate, 1976). Represented by several taxa that together show a general trend towards an increase in size, flightlessness, and foot-propelled



**Fig. 6.** Skeletal reconstructions of the Late Cretaceous hesperornithiform *Baptornis* and its much larger relative *Hesperornis*.

diving specializations, these birds have been recorded over much of the Northern Hemisphere and across a vast latitudinal extent – from the Arctic Circle to the Gulf of Mexico – and from depositional environments ranging from offshore to fluvial (Galton and Martin, 2002). Hesperornithiforms are also the first birds for which a modern type of skull kinesis (prokinesis) can be confirmed (Bühler *et al.*, 1988). Throughout their history, they evolved a suite of foot-propelled diving specializations, including long and slender pelves, densely packed bones, very short femora, knees bearing enormous lever-like patellae, and large feet with toes able to rotate sideways. Histological studies of their bones have also shown that unlike more primitive birds, hesperornithiforms had growth rates similar to their modern counterparts, thus suggesting that the elevated rates characteristic of neornithines developed early in ornithurine history (Chinsamy *et al.*, 1995; Padian *et al.*, 2001; Chinsamy, 2002).

The earliest known hesperornithiform is the 100 million-year-old *Enaliornis* from England (Galton and Martin, 2002), a taxon known from disarticulated remains. Slightly younger still is the Canadian *Pasquiaornis* (Tokaryk *et al.*, 1997), whose wing anatomy hints at rudimentary flying capabilities. However, by far the best represented taxa of these birds are those known from later Cretaceous (Turonian-Campanian) rocks from the North American Pierre Seaway, including the flightless *Baptornis* (Martin and Tate, 1976), *Parahesperornis* (Martin, 1984), and *Hesperornis* (Marsh, 1880) (Fig. 6). Some even younger hesperornithiforms are known from marine deposits of the Turgay Strait, a shallow seaway that bisected Eurasia, linking the Arctic Ocean with an equatorial basin, and connected shallow seas that flooded much of Europe. Known only from fragmentary bones, these terminal Cretaceous occurrences of marine hesperornithiforms from the Old World are identified as the large *Asiahesperornis* (Nessov, 1992) and *Hesperornis rossicus* (Rees and Lindgren, 2005). Contemporaneous records of small members of the group have also been reported from fluvial rocks of Central Asia (Kurochkin, 2000).

From many of the same environments as the hesperornithiforms comes the historically well-known Late Cretaceous seabird *Ichthyornis* (Marsh, 1880). Although originally considered to comprise a series of closely related taxa, recent revisionary work has clarified taxonomic problems associated with a large collection of specimens collected in the 19th century, and has shown that these are likely members of just the single species, *Ichthyornis dispar* (Clarke, 2002) (Fig. 7). As a matter of fact, one of the several original species types (i.e., *I. victor*) has been shown to be a chimera formed by numerous specimens, some even of taxa that may be closer to modern avians (Clarke, 1999, 2002). In most aspects of its skeleton, the flying *Ichthyornis* is anatomically modern, albeit still toothed. In recent times, this taxon has consistently been regarded as an immediate relative of modern avians (Fig. 1). Its specimens have been collected from marine and brackish deposits across North America (Feduccia, 1999) and remains of alleged close relatives were reported from 90 million-year-old similar environments in Uzbekistan (Nessov, 1992). A range of sizes are represented among the known North American specimens – some are 20 percent larger than others – illustrating a general trend towards larger size over the 15 million years (early Turonian-early Campanian) of the known history of *Ichthyornis*. Whether this large size range is significant taxonomically remains unclear and will to a great extent depend on interpretations of the growth physiology of this bird (Clarke, 2002).

## EARLY NEORNITHINE DIVERGENCE: THE RISE OF MODERN BIRDS

*Ichthyornis* is certainly very intimately related to modern birds, Neornithes, but ongoing studies are revealing taxa that seem to be even more closely related. A number of anatomically modern Late Cretaceous avians – *Limenavis* (Clarke and Chiappe, 2001), *Apatornis* (Clarke, 2004), *Iaceornis* (Clarke,

2004), and others (Dyke *et al.*, 2002) – appear to be closer than *Ichthyornis* to the ancestry of extant birds. Since the 19th century, a long list of Cretaceous fossils have been classified within the neornithine lineages themselves (e.g., Marsh, 1873, 1880; Shufeldt, 1915; Brodkorb, 1963; Hou and Liu, 1984; Kurochkin, 1985; Elzanowski and Brett-Surman, 1995; Hope, 1999, 2002; Howard, 1955; Tokaryk and James, 1989; Nessov, 1992; Olson, 1992; Noriega and Tambussi, 1995; Stidham, 1998; Kurochkin *et al.*, 2002). These fossils are generally fragmentary and most of them are represented simply by isolated bones. The essentially modern anatomy of these fossils has led to the notion that some neornithine lineages (e.g., charadriiforms, pelecaniiforms, galliforms, anseriforms, gaviiforms) diversified in pre-Tertiary times (e.g., Martin, 1984; Cracraft, 1986; Chiappe, 1995; Padian and Chiappe, 1998; Feduccia, 1999; Hope, 2002) although this perception has not received confirmation from genealogical studies – based on cladistic methodology – of the most complete fossils (Clarke and Chiappe, 2001; Dyke *et al.*, 2002). An exception to this trend of fragmentary, supposedly Cretaceous 'neornithines' is the recently published *Vegavis* (Clarke *et al.*, 2005) from the Late Cretaceous of western Antarctica. *Vegavis* represents the first skeleton complete enough to be placed unambiguously within a modern clade of birds, Anseriformes (screamers, ducks and geese) (Clarke *et al.*, 2005). Support for the Cretaceous differentiation of a diversity of neornithines has also been defended on the basis of temporal calibrations of genealogical hypotheses of living birds as inferred from their genetic makeup (e.g., Cooper and Penny, 1997; van Tuinen and Hedges, 2001; Paton *et al.*, 2002). These molecular studies have supported a pre-Tertiary radiation, or in-

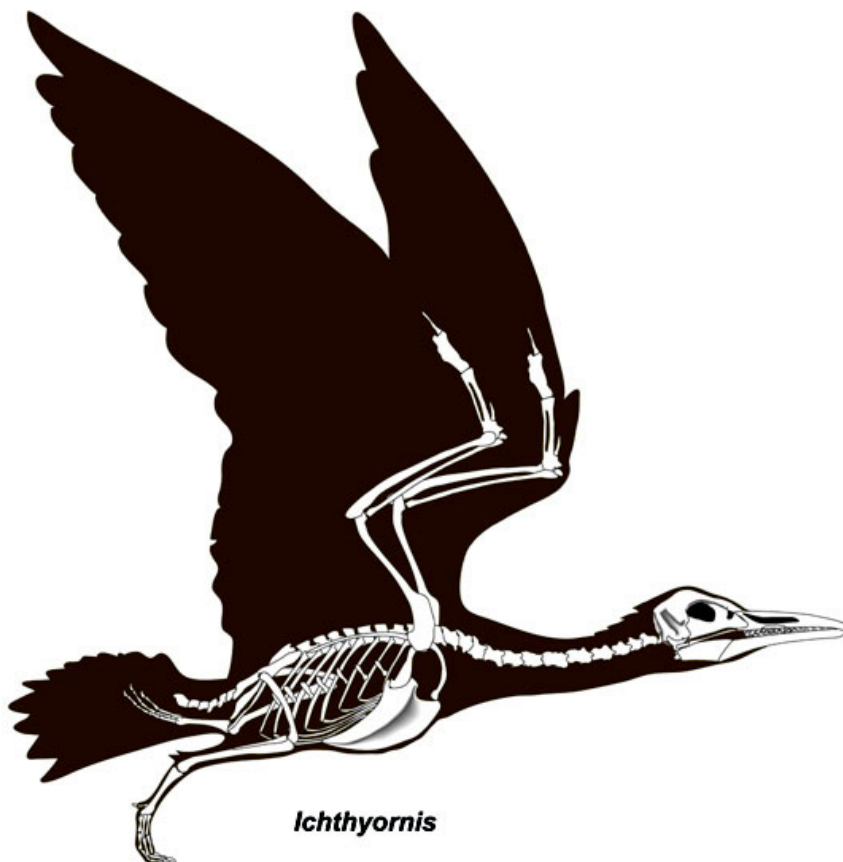


Fig. 7. Skeletal reconstruction of the Late Cretaceous *Ichthyornis*.

itial diversification, for at least ratites (ostriches, rheas, and their kin; van Tuinen and Hedges, 2001), parrots (Miyaki *et al.*, 1998), songbirds (Barker *et al.*, 2002), landfowl (van Tuinen and Dyke, 2004), and shorebirds (Paton *et al.*, 2002). Despite some of these inferences being based on doubtful calibration and limited gene or taxon sampling (Dyke, 2001; Dyke and van Tuinen, 2004; van Tuinen and Hedges, 2004), a contentious debate has been engendered (Dyke, 2003; Feduccia, 2003; van Tuinen *et al.*, 2003). The extreme viewpoints of this controversy are taken, on the one hand, by paleontologists reading the fossil record primarily at face value (e.g., Feduccia, 1999, 2003) and on the other hand, by molecular systematists who either disregard the fossil record or use it uncritically, outside a genealogical framework (e.g., Cooper and Penny, 1997). Both viewpoints envision a Cretaceous origin for the group, but while one endpoint hypothesis argues that most primitive neornithines survived the terminal Cretaceous extinction and gave rise to an 'explosive' radiation in the earliest Tertiary (Feduccia, 1995, 1999, 2003), the other endpoint hypothesis supports a much earlier origin for the group with most divergences occurring during the Mesozoic (Cooper and Penny, 1997; van Tuinen and Hedges, 2001). No solution to this debate is likely to be forthcoming, but it is likely that a middle ground between both extreme positions will turn out to be correct. The discovery of *Vegavis* suggests that at least some major divergences of neornithines (anseriforms, galliforms, and paleognaths) must have diverged in pre-Tertiary times and the temporal proximity to the K-T boundary of birds confidently placed within a much greater diversity of modern lineages also implies a substantial degree of differentiation prior to the end of the Cretaceous. Perhaps, as has been suggested, some clades of modern birds did originate deep in the Cretaceous but maintained a low Mesozoic diversity (Cooper and Fortey, 1998). Indeed, it could also be the case that much of Cretaceous neornithine evolution took place in the Southern Hemisphere, from where the fossil record has been far less thoroughly sampled (Cracraft, 2001). Yet arguments for an extensive Early Cretaceous divergence are at odds with the complete absence of anatomically modern fossils from a number of well-sampled deposits containing the abundant remains of more basal birds, and other small vertebrates (Benton, 1999). The bottom line in this debate is that birds themselves are no longer rare in the Cretaceous (more than 30 taxa alone are known from the Early Cretaceous; Chiappe and Dyke, 2002; Chiappe and Witmer, 2002) but so far nothing that can be considered anatomically modern has ever been found prior to the terminal stages of the Cretaceous.

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## 초기 조류의 진화

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**요약:** 포유류, 도마뱀류보다 거의 두 배가 많은 약 10,000종 이상이 살고 있는 조류는 가장 다양성이 높은 현생 육상 척추동물이다. 그러나 이러한 굉장한 다양성의 기원은 남부 독일에서 발견된 1억 5천만년 전의 시조새 화석까지 거슬러 올라간다. 초기 조류 진화사 연구와 비행 능력의 획득은 진화 개념의 출현부터 고생물학의 가장 큰 화두가 되어왔다. 그러나 최근까지도 주로 해안과 바다환경에서 발견된 제한된 적은 수의 화석만이 있었고 이들 화석들은 해부학적으로 시간적으로 커다란 단절이 있었다. 지난 20년에 걸쳐 백악기 조류화석이 폭발적으로 발견됨에 따라 그 당시 기대하지 않았던 조류의 다양성이 밝혀졌다. 1990년대 초부터 지난 20년간 발견된 수보다 3배나 많은 새로운 종이 기재되었다. 발견의 빈도가 빠르게 증가함에 따라 이전에 존재했던 해부학적 시간적 단절의 많은 부분이 채워졌을 뿐만 아니라 초기 조류화석의 연구는 척추고생물학의 가장 활발한 분야 중 하나가 되었다.

**주요어:** 진화, 중생대, 조류

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