

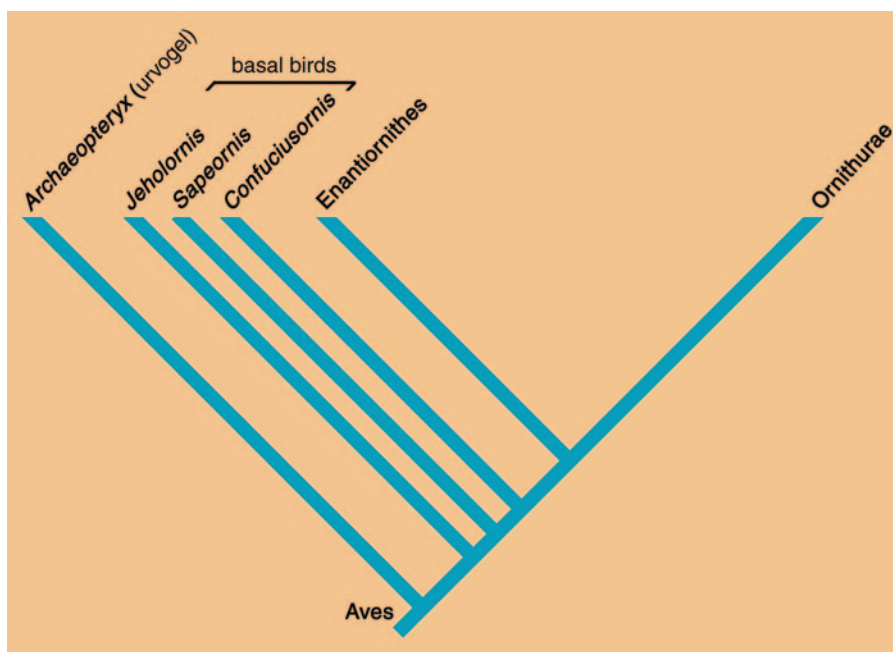
# Mesozoic aviary takes form

Alan Feduccia\*

Department of Biology, University of North Carolina, Chapel Hill, NC 27599-3280

When I attempted a modern synthesis of avian evolution in 1980 (1), I told the then science editor at Harvard University Press that I thought the information on avian evolution was coming in so sluggishly that there would be little need for a quick revision. Was I ever wrong! By the early 1980s, the revelation of the presence of volant paleognaths in the Northern hemisphere Paleogene (2) provided compelling evidence that ratites were not ancient passengers on drifting continents, but the product of a post-Cretaceous–Tertiary radiation from ancestors that for the most part flew to their respective continents. In the same year, an initially muted epiphany appeared with the dramatic discovery by Cyril Walker (3) of the existence of a completely unknown subclass of Mesozoic birds, which he called the enantiornithines, or opposite birds, so-called because the fusion of their tarsal elements was the opposite of that of ornithurine (modern-type) birds; they also possess a distinctive arrangement of the bones of the shoulder girdle and a unique sternum. The story of Mesozoic birds became complicated by the discovery in 1985, by Russian colleague Evgeny Kurochkin (4), of *Ambiortus*, a Lower Cretaceous archaic but modern-type ornithurine (carinate) bird with an advanced flight apparatus. However, Walker's discovery was followed by the discovery of additional enantiornithine or opposite birds from the Lower Cretaceous of Spain (5). In addition, at the 1992 meeting of the Society of Avian Paleontology and Evolution in Frankfurt, Germany, a young Chinese paleontology graduate student appeared for the first time and dazzled the conference participants with discoveries of a major radiation of opposite birds from the Early Cretaceous of China, represented by some 20 individual specimens belonging to at least three distinctive taxa. Zhonghe Zhou's discovery (6) was to lead the way to one of the most dramatic breakthroughs in avian evolution that followed during the ensuing years.

This window on the Early Cretaceous via the Chinese Jehol Biota ranks with only a handful of such deposits, including the Late Jurassic Solnhofen Limestone, that has given us relatively complete pictures of the biota of a particular time in the past and has revealed a relatively complete fauna of the world of the Early Cretaceous (7). In a recent



**Fig. 1.** Simplified diagram of putative phylogenetic relationships of the major groups of the Mesozoic aviary discussed here (and excluding the more problematic avian microraptors and flightless bird *Caudipteryx*). The time of branching of the ornithurines remains a major question. (Modified from ref. 15.)

issue of PNAS, Zhou continued his remarkable discoveries with colleague Fucheng Zhang (8), describing one of the most dramatic discoveries from the Chinese Early Cretaceous, a complete skeleton of *Hongshanornis*, the earliest known beaked ornithurine bird (archaic but modern-type bird), coeval with opposite birds (enantiornithines) from the same deposit. *Hongshanornis* was a small bird with strong flying capability and shows again the antiquity of modern avian flight architecture, only some 20 or so million years after the earliest known bird, the urvogel *Archaeopteryx*, as well as size reduction characteristic of more modern lineages.

Given the fact that the number of new species of Mesozoic birds discovered during the past decade more than triples those described during the past 200 years, one can begin to have some degree of confidence in reconstructing their history. Although a number of disparate interpretations have appeared, a fairly clear picture emerges from the ongoing controversy. In 1983 and later in 1995, Martin (9, 10) noted the distinctiveness of the enantiornithines from the ornithurines, and their worldwide Cretaceous distribution indicated that they were the dominant landbirds of the

Mesozoic. He included the enantiornithines along with *Archaeopteryx* within a subclass Sauriuriae, as distinctive from the subclass Ornithurae, or birds of modern aspect. [The skull of *Archaeopteryx* is extremely similar to that of enantiornithines, particularly *Cathayornis* (11).] Since then, archaic birds that do not fit clearly into a taxonomic group have been described, including the primitive beaked bird *Confuciusornis*, the seed-eating bird *Jeholornis* (with only three small teeth in the lower jaw), and *Sapeornis* (with no lower jaw teeth), thus bringing into question the exact position of *Archaeopteryx*. Nevertheless, with the present description of the ornithurine *Hongshanornis*, the evidence appears overwhelming that “Early Cretaceous bird evolution highlights a distinctive dichotomy between enantiornithines and ornithurines, the two major avian groups of the Mesozoic” (ref. 8; see also Fig. 1), a proposal that has been only weakly contradicted by a

Conflict of interest statement: No conflicts declared.

See companion article on page 18998 in issue 52 of volume 102.

\*E-mail: feduccia@bio.unc.edu.

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taxon from the Late Cretaceous (12), at a time when homoplasy may be at play.

These two major clades of the Age of Reptiles were also distinctive in many other ways, and notably studies of long-bone histology show that enantiornithines and more basal birds still retained growth rings, grew slowly, and were likely ectothermic to a large degree. In contrast, the bone histology of Cretaceous ornithurines is similar to that of modern birds, devoid of growth rings (13). Such bone growth is suggestive of an endothermic physiology, a corollary of strong flight and migratory ability, perhaps associated with a shore-line habitat in Cretaceous ornithurines. Interestingly, *Hongshanornis* shows skeletal features that indicate a shore-dwelling habitat, conforming to what we know of many of the other Mesozoic ornithurines, especially the late Cretaceous ichthyornithiforms and hesperornithiforms. All but one of the enantiornithines is known from lacustrine or terrestrial habitats. Although speculative, it may be that the advanced physiology of ornithurines (advanced flight capability and

endothermy) adapted this clade for the physiologically demanding shore-line ecosystem. Physiological differences may also explain why the enantiornithines became extinct along with the dinosaurs at the end of the Cretaceous, whereas

## Bone histology of Cretaceous ornithurines is similar to that of modern birds.

the ornithurines by the end of the Cretaceous had produced the font of the modern, post-Cretaceous–Tertiary, avian radiation.

It is also clear that teeth were reduced and replaced by a beak several times in the Cretaceous ornithurines, as well as in some primitive lineages (*Confuciusornis*). In addition, another revelation is that Early Cretaceous ornithurines possessed a predeontary bone

in front of the dentaries, previously known only in late Cretaceous ornithurines (ichthyornithiforms and hesperornithiforms), and this character is very likely a synapomorphy of the clade, although it is also an independent character uniting the dinosaurian clade Ornithischia.

To date, there is simply no evidence, either structural or biological, for the existence of any form of protofeather (14). Nevertheless, thanks to the careful work of Zhou and Zhang (8) and others, the field of Mesozoic birds has made great strides, and the current discovery will go a long way toward clarifying what has been a murky picture of the avian past. We can now minimally say that the aviary of the Age of Reptiles comprised a number of basal groups, but was characterized by two major clades, the archaic land birds or enantiornithines (opposite birds), and the primitive ornithurines (birds of modern aspect), the totality of which produced an ancient adaptive radiation with a surprising morphological diversity, analogous in many respects to the diversity of modern birds.

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