Explosive Evolution in Tertiary Birds and Mammals

Alan Feduccia

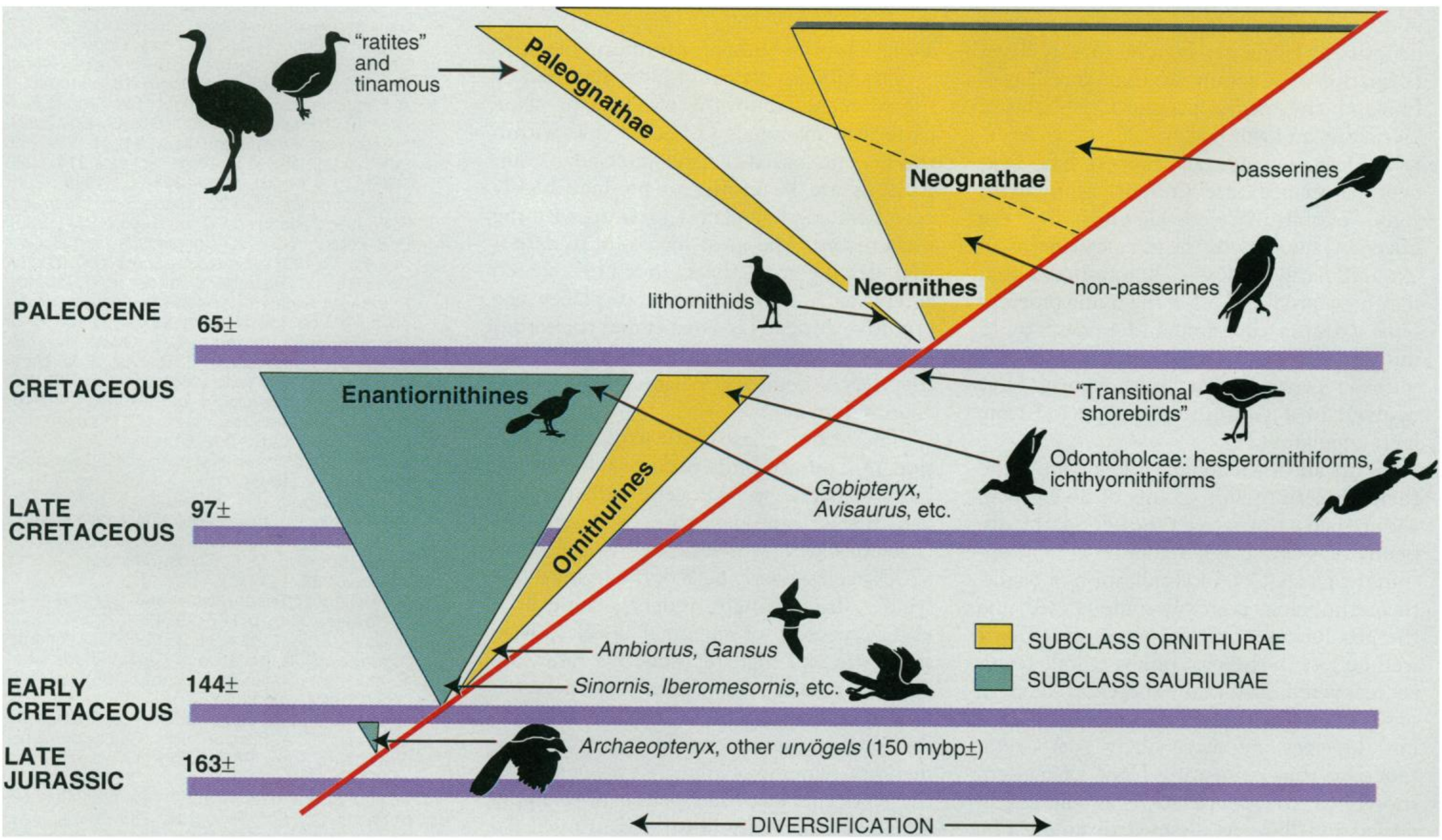
The traditional view of avian evolution over the past century is that of sluggish gradualism, in which many living orders of birds are thought to have originated from the mid-Cretaceous or so (*1*), and, passing unblemished past the Cretaceous-Tertiary (K-T) boundary, slowly diversified into the present avian morphological landscape. Thomas Huxley in 1867, for example, viewed the living ratites, such as ostriches and their allies, as "waifs and strays" of the primeval radiation. As a consequence, numerous authors (*1*, *2*) have attempted to explain current biogeographic patterns of numerous avian lineages by drifting continents, a mechanism known as vicariance biogeography. For instance, Sibley and Ahlquist in their analysis based on DNA-DNA hybridization (*1*, p. 701) stated that, "We have assumed that the divergence between the lineages that produced the living ostrich and rheas was caused by the opening of the Atlantic, and we assigned a date of [about] 80 million years ago to that event." Although ratitelike morphology has been shown to have evolved in flightless Hawaiian gooselike ducks or moa-nalos (for example, *Thambetochen*) (*3*), which can be no older than some 4 million years, it has been assumed that ratites could only have come from the Mesozoic.

The author is in the Department of Biology, University of North Carolina, Chapel Hill, NC 27599–3280, USA.

Recent discoveries have revolutionized our view of bird evolution during both the Mesozoic (*4*) and Cenozoic (*5*), so that a new broad hypothesis can now be established, that offers a radical departure from the time-honored phylogenetic picture. According to this model, birds endured massive late Mesozoic extinctions, underwent a dramatic K-T bottleneck, and closely paralleled mammals in their explosive phyletic evolution in the early Tertiary.

The first departure from tradition came from the discovery of the Mesozoic enantiornithine birds, or "opposite birds" (*6*), a newly revealed clade characterized by the opposite fusion of the three tarsal elements. In modern birds the developmental fusion is from distal to proximal; in opposite birds, it is proximodistal, and the triosseal canal (which accommodates the ligament responsible for the wing's upstroke) is formed by a distinctive bony configuration. Except for a long pygostyle (fused caudal vertebrae) instead of a long, reptilian tail, opposite birds closely resemble the late Jurassic *Archaeopteryx* in the toothed skull and the primitive pelvic region. However, the fully volant flight apparatus in enantiornithines is precocious and greatly advanced over that of *Archaeopteryx*. Most of the fossils thought previously to be modern lineages in the Mesozoic are now known to belong to the opposite birds (*7*). These were the dominant landbirds of the Mesozoic, and few, if any, modern orders as we know them today existed in the late Cretaceous.

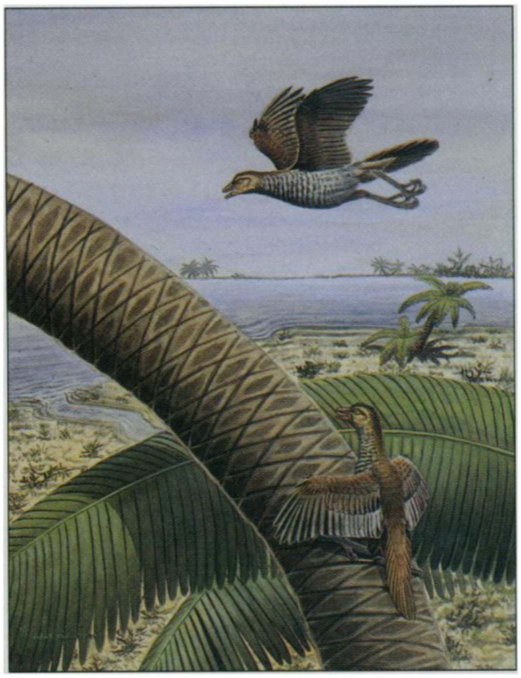
The discovery of these birds in the early Cretaceous of China by Zhou (*8*) illustrates that along with the modern-type ornithur-



New view of avian evolution. Enantiornithines (opposite birds) were the dominant landbirds of the Mesozoic but coexisted with modern-type ornithurine birds in the early Cretaceous. *Archaeopteryx* may be closely allied with the enantiornithines, and together, they constitute the subclass Sauriurae. After the late Cretaceous extinctions, the ornithurine birds began a modern, explosive adaptive radiation, almost all orders appearing within a period of 10 or so million years. By the Miocene, passerines became the predominant landbirds. Silhouettes not to scale.

ine bird *Ambiortus* (9), from the early Cretaceous of Mongolia, the two major lineages of birds, subclasses Sauriurae (enantiornithines + *Archaeopteryx*) and Ornithurae, were coeval in early Cretaceous. None of the opposite birds survived the K-T boundary, and along with well-known Cretaceous ornithurine birds, the toothed hesperornithiforms and ichthyornithiforms, became extinct. Whether the extinctions were the result of gradual geologic and climatic change or an extraterrestrial cataclysm, it is apparent that the K-T extinctions were as dramatic in birds as in other organisms.

Modern orders thought to be represented in the late Cretaceous have been restudied (*10*), and all belong to what are termed "transitional shorebirds," which represent the bottleneck of avian morphotypes transcending the K-T boundary, and must, like the mammalian insectivores, represent wellsprings of the new Tertiary adaptive radiation of birds. This is evidenced by discovery of a number of shorebird–modern order mosaics in the Eocene: *Juncitarsus*, *Presbyornis*, and *Rhynchaeites*, which are shorebird-flamingo, shorebird-duck, and shorebird-ibis mosaics, respectively. As corroborated by massive fossil finds from such disparate deposits as the early Eocene Green River Formation of Wyoming and London Clay of England, the medial Eocene Oil Shales of Germany, and the Eocene-Oligocene deposits at Quercy, France, all orders of birds (except passerines) are present, along with some evolutionary dead ends, by the Eocene. This can only be characterized as an extraordinarily explosive evolution, one that may have produced all of the living orders of birds within a time frame of some 5 to 10 million years, closely paralleling that described recently for whales, thought to have evolved in a 10-million-year period from land ungulates (*11*).



Life reconstruction of the sparrow-size "opposite" or enantiornithine bird *Iberomesornis* from the lower Cretaceous of Spain. The skull, pelvic girdle, and hindlimbs are primitive and quite similar to *Archaeopteryx*, but instead of a long, reptilian tail, the caudal vertebrae are fused into an elongated pygostyle, and the advanced flight apparatus was that of a fully volant bird. Enantiornithines are known primarily from lacustrine deposits. [Painting by John P. O'Neill]

With all of the avian orders coming off their phyletic nodes (points of divergence) within such a restrictive time period, the difficulty of ascertaining higher level relationships by DNA-DNA hybridization or cladistic methodology is grossly compounded, and the resolution of avian phylogenies may well be lost to the past unless telltale fossils are recovered, such as the shorebird–modern order mosaics. Indeed, the modern shorebird lineages are most likely post-Cretaceous, so that comparing DNA of modern shorebirds to groups such as flamingos, ducks, and ibises is doomed to failure (*1*); likewise, cladistic analyses have shown little progress (*12*), grouping phylogenetically disparate, but convergent look-alikes such as hawks and owls and loons, grebes, and ancient toothed hesperornithiform birds.

The modern genera of birds appeared by the Miocene, following roughly the same pattern as mammals (*13*), and it is within the genera that successful molecular comparisons are beginning to produce highly corroborated phylogenies, agreeing with the fossil record. The most successful to date is that dealing with the cranes (*14*), which agrees with morphology and places the primitive African crowned cranes (*Balearica*) in a basal position. It is at the generic level that DNA comparisons are likely to encounter success.

The second phase of the explosive radiation of Tertiary birds occurred during the late Oligocene and Miocene with the sudden rise of the passerine or song birds (Passeriformes), which now constitute some 5700 species, nearly 60% of the living avian species. Interestingly, rodents, some 40% (1700 species) of mammal species, with small size and high reproductive rates, appear to parallel the avian passerines but evolved somewhat earlier in the Tertiary. Although passerines are known from fragmentary remains of slightly earlier epochs, the Miocene was their period of triumph. This is dramatically illustrated in fossil deposits in Europe where passerines are generally absent in the Oligocene and then are recovered in excess of all other fossil birds in certain Miocene deposits (*15*).

Many questions remain, but a general picture of bird evolution is emerging. It illustrates that birds, like many other groups, underwent an initial Mesozoic adaptive radiation of archaic types, were submitted to a late Cretaceous demise and subsequent bottleneck, and underwent a dramatic reorganization in the early Tertiary, perhaps with initial landbird and shorebird descent. This explosive evolution paralleled that of mammals, producing all the modern lineages of birds within about 10 million years, yielding modern orders by the Paleocene and Eocene, modern families by the late Eocene or early Oligocene, and modern genera by the Miocene. A second phase of explosive radiation produced myriad passerines by the late Tertiary. If this new picture is correct, then scores of papers attributing modern bird biogeography to drifting continents will have to be redrafted, and molecular clocks based on these assumptions must be reset.

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