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EARLY EVOLUTION OF BIRDS: the debate over the origin of birds has been renewed in recent years after many decades of relative quiescence. There never has been any question that the late Jurassic fossil *Archaeopteryx lithographica* is the closest relative of all modern birds, (see ARCHAEOPTERYX), but opinions differ as to which group of archosaurs, the crocodiles, thecodonts or theropod dinosaurs, is most closely related to the avian lineage. The classic work of Heilmann in the 1920s suggested a thecodont ancestry, quite independent of those lineages which led to the crocodiles or to the sauropod and theropod dinosaurs. This traditional view has been challenged by Ostrom, who has argued that the avian lineage (including *Archaeopteryx*) is most closely related to theropods. He cites an impressive list of shared similarities in the postcranial skeleton in support of his claim. A third view is that *Archaeopteryx* and modern birds are more closely related to crocodiles than to theropods. At present the theropod hypothesis is to be preferred, if only because of the greater volume of evidence marshalled by Ostrom (1974, 1976).

With respect to our attempts to understand the biological transformations that took place between 'reptiles' and modern birds, it may not matter which of the above hypotheses we accept, because the most relevant source of evidence for inferring these transformations would seem to be *Archaeopteryx*. But the problem remains: how are hypotheses about the origin of birds to be tested? The structure of *Archaeopteryx* can be reconstructed and inferences can be made about its functional-mechanical characteristics. From this, 'scenarios' about the transformation to the modern avian condition can be created, but must be subject to critical evaluation, i.e. it must be possible to reject them, even if only by challenging the consistency of the arguments, since the chances of testing them empirically are small. Ostrom's hypothesis about the origin of flight is a case in point. He postulates that *Archaeopteryx* and its close relatives were primarily terrestrial predators and in pursuit used their feather-covered forelimbs as 'insect nets'. Such behaviour and morphology, he theorizes, 'pre-adapted' this lineage for powered flight. The traditional hypothesis is that an arboreal *Archaeopteryx* developed the ability to fly by parachuting and gliding between trees or to the ground. *Archaeopteryx* itself does not provide compelling evidence against either hypothesis. The latest interpretations suggest that *Archaeopteryx* possessed moderate aerodynamic capabilities, if not powered flight, but this is consistent with either a terrestrial or arboreal origin of flight. If *Archaeopteryx* is interpreted as arboreal, one could argue that its ancestors were terrestrial and already had the power of flight (Ostrom's hypothesis); if *Archaeopteryx* is interpreted as being primarily terrestrial, acquisition of arboreal habits could still be necessary for the evolution of an aerodynamic capability. Actually, the structure of *Archaeopteryx* does not seem designed exclusively either for a terrestrial or an arboreal existence, further complicating the issue. Any preferred hypothesis could be saved from falsification by shifting the postulated events backward or forward in time. Thus, such narrative-type scenarios on evolution of FLIGHT, homeothermy, origin of FEATHERS or other characteristics can scarcely be scientifically tested. Phylogenetic hypotheses, on the other hand, are rigorously testable in that they can be supported or not by analysis of new

characters or new taxa. Some of these hypotheses, and their implications for the early history of birds, are considered below. It must be stressed that opinions on almost any hypothesis differ widely, that few critical evaluations have been published and that space does not permit extensive description of the evidence for or against.

One major lineage, comprising the divers, grebes, penguins, petrels, shearwaters and allies, may be one of the basal groups of birds. The divers, grebes and several Cretaceous diving birds, including *Hesperornis*, share many unique characteristics of pelvis, hindlimb and skull. Relationship of those groups to the penguins is supported by similarities of skull, sternum and pelvis. Pelecaniforms and procellariiforms seem to be good monophyletic taxa and similarities in their skull morphology suggest that they may be sister groups and related to the diving birds and penguin lineage, thus forming a single large aquatic assemblage.

Further, A.C. Wilson and his colleagues have argued that these aquatic groups share a general similarity in their proteins that sets them somewhat apart from other avian lineages. Also it has long been accepted, though without compelling evidence, that penguins and procellariiforms might be closely related.

This hypothesis involves interesting implications. First, this lineage must extend back to the beginnings of avian history. The extinct diving group, the enaliornithids, is related to divers, grebes and hesperornithids. *Enaliornis* is found in lower Cretaceous deposits, which implies that the common ancestors of the lineages leading to the diving birds and penguins on the one hand, and to pelecaniforms and procellariiforms on the other, are older, extending virtually back to the time of *Archaeopteryx*, much further than previously suspected. (This does not mean that the recent families of these orders are as old.)

Secondly, the hypothesis indicates that an early evolutionary line produced an entirely aquatic radiation, thus implying that each did not occupy that environment independently.

Thirdly, the hypothesis implies the loss of reptilian features such as teeth independently in at least two lineages. *Hesperornis* possessed teeth and, if this genus is related to divers and grebes, it can be inferred that teeth were lost in the latter lineage. Likewise *Ichthyornis*, the other late Cretaceous genus known to have teeth, may be more closely related to the charadriiforms than to any other group; this implies a second independent loss of teeth in charadriiforms.

A second group, the 6 orders of ratite birds and the tinamiforms (tinamous) were considered to be very primitive unrelated taxa, with separate ancestral stocks flying to the far-flung southern continents, evolving there in isolation to produce distinct lineages of large flightless birds. But much recent morphological, behavioural and biochemical data indicate that these birds comprise a monophyletic group. One hypothesis unites the South American rheas and African ostriches, on the one hand, with the Australian cassowaries and emus on the other. These 4 groups are related to the elephant birds of Madagascar, and all 5 in turn to the moas and kiwis. Finally, the ratite assemblage is most closely related to the Neotropical tinamous, capable of flight.

Much can be inferred from this hypothesis. First, because of their relationship to the tinamous, and because they possess features (e.g. pygostyle, alula) associated with flight, the palaeognaths were not primitively flightless; this contrasts with the old view that ratites were intermediate between reptiles and 'true' birds. Secondly, the ratites became flightless once, rather than many times independently. Thirdly, large body size evolved only once, soon after the ratite lineage separated from that of the tinamous, the kiwis apparently representing a secondary reduction. Not only are the closest relatives of the kiwis, the moas, of medium to very large size, but kiwis also lay an egg that is the largest relative to body size of any bird.

The hypothesis of ratite monophyly correlates well with what is known about continental drift and the timing of the break-up of the continents. It is thus possible to erect a fairly simple hypothesis regarding the biogeographic history of the ratites, involving continental fragmentation, isolation of once widespread ancestral populations, and subsequent evolution of the various taxa.

To what extent were the ratites and tinamous a part of the basal radiation of birds? A satisfactory answer will come only when an hypothesis has been presented and corroborated regarding their closest relatives among the remaining non-passerine birds. At present there is little or no evidence supporting the earlier view that ratites represent the sister-group of all other birds (although some biochemical data are said to point to this position). Ratites and tinamous seem just as advanced

morphologically as other non-passerine groups, and thus it may be they are related to some non-passerine taxon fairly far removed from the basal radiation of birds.

Recently a small number of phylogenetic hypotheses, interrelating avian orders, have been proposed which, if corroborated by further evidence, may give increasing knowledge about the early evolution of birds. Most of these hypotheses are highly controversial and all the evidence has not yet been published. Nevertheless, it is useful to summarize their findings because they provide the best picture we have of avian evolution.

The Charadriiformes (shorebirds, gulls, and allies) are undoubtedly a very old group, extending well into the Cretaceous. Interrelationships within the order are a matter of some dispute and await a well-corroborated hypothesis. The Gruiformes (cranes, rails, and allies) have been considered as related to charadriiforms, possibly on the basis of a general similarity seen between the gruiform bustard-quails and plains-wanderers (Turnicidae) and some charadriiform groups, such as the seed-snipe (Thinocoridae) or the pratincoles and coursers (Glareolidae); and the similarity of the latter family to the sandgrouse and pigeons has suggested a close relationship between columbiforms and charadriiforms. If eventually these 3 groups are seen to have close ties with one another, the relationship very possibly would define one of the major early radiations within birds.

Recently, Feduccia (1976) and Olson (1978) have suggested that flamingos (Phoenicopteridae) are not related to ciconiiforms but to avocets and stilts (Recurvirostridae) within the charadriiforms. This hypothesis is based on some osteological similarities between the 2 groups and on a general similarity in breeding habits between flamingos and the Australian Banded Stilt *Cladorhynchus*. But there are data from osteology, myology, and biochemistry in conflict with their scheme of relationships and consistent with the view that recurvirostrids are advanced charadriiforms and that ciconiiforms comprise a monophyletic assemblage.

Another phylogenetic hypothesis links the ducks, geese, and swans (Anseriformes) and the pheasants, grouse, and their allies (Galliformes). That these are sister-groups is suggested by shared similarities, interpretable as derived, in their skull morphology and behaviour, as well as a general similarity in their biochemical make-up. On the basis of an electrophoretic analysis of egg-white proteins, Sibley and his colleagues (1972) postulated that the Hoatzin (*Opisthocomidae*) is not related to galliforms but to cuckoos (Cuculiformes). Conflicting evidence, both from morphology and the immunological examination of their proteins, suggests that the Hoatzin may not be related to cuckoos but is instead the sister-group of the other galliforms. Whichever hypothesis about *Opisthocomus* is correct, the relationship between anseriforms and galliforms involves two orders in which the history of the primitive families seems closely tied to the break-up of the southern continents by continental drift. This implies that their ancestry extends back into the Cretaceous. For example, within the galliforms the Hoatzin is South American in distribution; the next most primitive group, the megapodes, is found in Australasia; and the next most primitive group after the megapodes, the cracids, is primarily South American. Within the anseriforms, the primitive sister-group of the ducks, geese, and swans is the screamers (Anhimidae) of South America, whereas the most primitive member of the Anatidae, the Magpie Goose *Anseranas*, is Australian. These relationships imply trans-Antarctic relationships between South America and Australia, a common biogeographic pattern in plants and animals.

There is as yet no compelling evidence to suggest a relationship between the anseriform-galliform lineage and any other order. Several candidates have been suggested, including the ratites and tinamous and also the ciconiiforms. Once a corroborated hypothesis is put forth, it will almost certainly define a major lineage in avian history extending well back into the Cretaceous.

Most of the more 'advanced' non-passerine groups cannot be viewed amongst the earliest of avian lineages, but a consideration of alternative phylogenetic hypotheses and our present knowledge of avian paleontology strongly suggest that most of these orders had their origins in the Cretaceous.

The interrelationships of the diurnal birds of prey (hawks, falcons, and their allies) and the owls (Strigiformes) have been controversial and debated for more than a century. Some well-known 19th century avian systematists, such as T.H. Huxley and F.E. Beddard, believed in a relationship whereas others, such as M. Fürbringer and H. Gadow,

thought owls to be closer to the nightjars and their allies (Caprimulgiformes). Some recent workers, most notably M. Jollie, hypothesize that the diurnal birds of prey are an unnatural group, composed of perhaps 4 separate taxa.

There are a number of unique osteological and myological characteristics uniting owls with at least some of the falconiform birds, and there are few similarities between owls and caprimulgiforms. To complicate matters further, some birds of prey, such as the secretary-birds (Sagittariidae) and New World vultures (Cathartidae), show no clear-cut relationships.

The origins of these orders must go back to a time in the Cretaceous. Virtually all of them have fossil representatives in the early Cenozoic, and thus the interordinal common ancestors were older still. Of considerable interest would be the discovery of the groups of non-passerine birds to which diurnal birds of prey and strigiforms, on the one hand, and caprimulgiforms on the other, are related. Such knowledge would help define several very old lineages within birds and provide much information about the evolution of the predatory life-style.

Two orders, the cuckoos (Cuculiformes) and the parrots (Psittaciformes), require brief mention. Both have been perennial enigmas as far as their relationships are concerned. Given the array of their possible relationships to other non-passeriform groups, both must be rather old, very likely Cretaceous.

All workers have recognized the orders Coraciiformes and Piciformes to be the most 'advanced' of the non-passerine birds and have considered the song-birds (Passeriformes) to be related either to one or the other, or to both. There is general agreement that the piciforms and passeriforms each constitute a monophyletic group, and equally that the coraciiforms may be an assemblage of unrelated taxa. Passeriforms have traditionally been related to piciforms but recent work suggests that passeriforms might be related to at least some coraciiform taxa. Moreover, the trogons (Trogoniformes) and mousebirds (Coliiformes) are also possibly related to some coraciiforms. The interrelationships of these groups are being studied by several systematists. In any case, fossil evidence already suggests that the common ancestors of these lineages must have been Cretaceous in age, although many of the recent families, particularly those in the Passeriformes, are almost certainly the results of Cenozoic radiations.

It can be seen from the preceding account that the interrelationships of the avian higher taxa are in a state of flux. Yet, it is equally obvious that this is a period of great excitement within avian systematics and that each year more and more is being revealed about the evolutionary history of birds. Once we have tested and corroborated hypotheses about the phylogenetic relationships of avian taxa, we can begin to answer a number of fascinating and important questions. For example, how many times did foot-propelled and wing-propelled diving evolve? How many different lineages of birds entered an aquatic environment? How many times did raptorial behaviour and morphology evolve?

In addition to these and other questions, phylogenetic hypotheses will also allow us to reconstruct the biogeographic history of avian taxa and relate that history to the paleogeographic and paleoclimatologic changes that took place in the Mesozoic and Cenozoic. One thing is almost certain to emerge from such analysis; avian phylogeny and biogeography are more intimately related to large-scale continental movements and climatic changes than previously realized.

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