The Ancestry of Birds

WALKER[1] has restated the long-held belief that both birds and crocodiles evolved from thecodont ancestors, but he added the novel suggestion that these two groups arose from a common thecodont ancestor and thus are much more closely related than has been previously realized. Inasmuch as the Thecodontia include the most primitive as well as the most ancient archosaurs known, it is highly probable that all subsequent archosaurs (including birds) were derived from members of this order. Although Walker may be correct, I do not think that the evidence cited indicates such a close relationship between birds and crocodiles as he proposes.

My purpose here, however, is not to challenge Walker's evidence or his interpretation of it. Rather, it is to present (in summary form) other evidence pertaining to the immediate (as opposed to the remote) ancestry of birds—evidence which has generally been ignored for the past 50 years.

The critical evidence of bird ancestry is preserved in the four presently known specimens of *Archaeopteryx*, which occupy a position much closer to avian origins than do the Triassic thecodonts mentioned by Walker. Before we can trace the remote origin of birds among thecodonts, we must be certain that we have correctly assessed the evidence in those specimens pertaining to the immediate ancestors of *Archaeopteryx*. With this in mind, during the past two years, I have studied all four *Archaeopteryx* specimens and currently I am preparing a detailed paper on the origin of birds. Walker's paper, however, has prompted this preliminary note, for in my opinion his theory can only be valid if it is totally consistent with a thecodont–coelurosaur–*Archaeopteryx*–Aves phylogeny. The skeletal anatomy of *Archaeopteryx* is almost entirely that of a coelurosaurian dinosaur—not thecodont, not crocodilian, and not avian.

The following coelurosaurian features of *Archaeopteryx* collectively are here considered as *prima facie* evidence of a coelurosaurian (Theropoda) ancestry of birds:

(*a*) Vertebral column: (1) Thoracic vertebrae pleurocoelous (and probably amphicoelous). (2) Ten cervical vertebrae and 12 to 15? thoracics.

(*b*) Fore limb: (3) Manus reduced to digits, I, II and III. (4) Phalangeal proportion of the fingers. (5) Proportions of the three metacarpals. (6) Carpus of two or three elements including a lunate radiale. (7) Proportions of humerus to radius and ulna. (The fore limb is not reduced in all theropods as has been frequently claimed; see for example *Ornitholestes*, *Velociraptor*, *Deinonychus*, *Ornithomimus* and *Deinocheirus*.) (8) Morphology of the humerus.

(*c*) Pectoral arch: (9) Very narrow, strap-like scapula. (10) Subrectangular coracoid fused to scapula.

(*d*) Hind limb: (11) Pes with four digits, V being lost. (12) Phalangeal proportions. (13) Reversed hallux. (14) Metatarsal proportions. (15) Mesotarsal joint. (16) Well developed ascending process of the astragalus. (17) Hind limb proportions. (18) Morphology of the femur.

(*e*) Pelvis: (19) Shape of the ilium. (20) Shape of the pubis, with a distal expansion and a long symphysis. (21) Open acetabulum.

In addition, it is possible that the pubis of the Berlin specimen (apparently preserved in the avian position) is dislocated and that it was originally directed ventrally or antero-ventrally as in theropods[2]. The proximal portion of that pubis is damaged, and the pubis of the Teyler specimen is oriented nearly perpendicular to the axis of the posterior thoracic vertebrae rather than obliquely as in the Berlin specimen.

Certain other non-avian characters present in *Archaeopteryx*, although perhaps primitive in origin are also typical of coelurosaurs. These are: (1) Long, unfused caudal series numbering at least 20 segments and apparently with elongated zygapophyses and chevrons. (2) Presence of gastralia. (3) Thecodont dentition. (4) Antorbital fenestra. (5) Probable presence of an external mandibular fenestra.

Many of these characters have been noted before, but two very important features have not. First, the lunate form of the radiale in *Archaeopteryx* has only recently been recognized in theropods (namely *Deinonychus*[3], *Stenonychosaurus*[4] and a recently collected specimen probably referable to *Velociraptor* (Kielan-Jaworowska, personal communication)). Second, the astragalus in *Archaeopteryx* has a well developed ascending process that apparently has not been noticed before, even though it is conspicuous in both the London and Berlin specimens.

These "coelurosaurian" characters of *Archaeopteryx* have in the past been attributed to parallel or convergent evolution, but the large number of features involved, and the complex nature of many of them, make this highly improbable. In my opinion, common ancestry alone cannot account for the overall coelurosaurian nature of *Archaeopteryx*.

No one any longer doubts the avian identification of these specimens—or their significance for the origin of birds, presumably because of the remarkable feather impressions. Yet they possess only two osteological characters that are exclusively avian, the furcula (preserved in the London and Maxberg specimens) and the possibly reverted pubis (doubtfully preserved in natural articulation only in the Berlin specimen). Indeed, if feather impressions had not been preserved all *Archaeopteryx* specimens would have been identified as coelurosaurian dinosaurs. The only reasonable conclusion is that *Archaeopteryx* must have been derived from an early or mid-Jurassic theropod.

A dinosaurian origin of birds is not a new idea, but it has been widely dismissed for the last 50 years because Broom[5] and Heilmann[6] concluded that coelurosaurs were not sufficiently primitive. The sole anatomical evidence cited by Heilmann for rejecting a coelurosaurian ancestry for *Archaeopteryx* was the absence of clavicles in all known theropods. Clavicles have been reported, however, by Camp[7] in *Segisaurus*, and by Osborn[8] in *Oviraptor*; furthermore a specimen, probable referable to *Velociraptor*, recently collected by a joint Polish–Mongolian expedition to the Gobi Desert (Kielan-Jaworowska, personal communication) also appears to possess clavicles. Regardless of these few occurrences, however, the absence of clavicles in theropods is only negative evidence and, in view of the fact that the clavicle is dermal in origin, its absence in fossil specimens has no phyletic significance. It may well have been membranous (but not lost) in most theropods and thus not preservable.

The most likely origin of so many coelurosaurian features in *Archaeopteryx* is by direct inheritance from a small coelurosaurian ancestor. The additional significance of this phylogeny is that "dinosaurs" did not become extinct without descendants and I suggest that feathers, as thermal insulators, could be the primary reason for the success of dinosaurian descendants. Can it be just coincidental that mammals succeeded as therapsid descendants (at least partly) because of a comparable adaptation—perhaps acquired at about the same time?

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