THE ORIGIN OF BIRDS: STRUCTURE OF THE TARSUS AND TEETH

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ABSTRACT.—The structure of the avian tarsus has recently been cited as evidence for the derivation of birds from theropod dinosaurs. Although birds and theropods have a long triangular ossification in front of the tibia and attached to the proximal tarsals, the morphological relationships of this bone are fundamentally different in the two groups. In modern birds and in all Mesozoic birds, this "pretibial" bone is a high, narrow structure associated primarily with the calcaneum, but independently ossified. The corresponding structure in dinosaurs is a broad extension of the astragalus.

Avian dentitions also pose a problem for the dinosaur hypothesis. While theropod teeth are serrated and have straight roots, avian teeth, like those of crocodilians, are unserrated, with constricted bases and expanded roots. *Received 17 July 1979, accepted 17 October 1979.*

OVER a century of research and debate concerning the problems of avian origins followed the discovery of the first *Archaeopteryx* skeleton in 1861 (von Meyer 1861). This literature has been summarized by Ostrom (1975a) and will not be reviewed here. The reptilian affinities of birds were pronounced as early as the 1860's by several authors, notably Parker (1864) and Huxley (1867). Since this time, virtually every major group of reptiles has been purported to be closely related, if not ancestral, to birds.

In more recent years two hypotheses have dominated the search for avian origins. A theory of their ancestry from Triassic pseudosuchian archosaurs grew from publications by Fürbringer (1888), Osborn (1900), and Broom (1913) and was later popularized by Heilmann (1926). Until about 1973, this hypothesis was accepted by the majority of ornithologists and paleontologists and was often cited in summary articles and textbooks. Since 1973, the pseudosuchian hypothesis has been largely replaced by a theory of direct derivation of birds from theropod dinosaurs, an old suggestion (Williston 1879) revitalized by J. H. Ostrom (1973–1979). The evidence compiled by Ostrom is extensive and first-hand, being based on studies of most of the original *Archaeopteryx* material.

In connection with our ongoing study of the Upper Cretaceous toothed birds (Martin and Tate 1976, Martin and Bonner 1977, Martin and Stewart 1977), we have re-examined the *Archaeopteryx* specimens and compared them with other Mesozoic birds and with various groups of reptiles. During these comparisons, we became aware of some weaknesses of the theropod argument and discovered new evidence that supports still another hypothesis, that of a close relationship between birds and crocodilians (Walker 1972, Whetstone and Martin 1979).

HOMOLOGY IN THE AVIAN TARSUS

Ostrom (1976a) has briefly described the tarsus (ankle joint) of *Archaeopteryx* and compared it with that of theropod dinosaurs. As with most reptiles, it has two proximal tarsal elements, a lateral calcaneum and a medial astralgalus. This division is apparent only on the right side of the Berlin specimen of *Archaeopteryx*, in which the two proximal tarsals are distinct and are apparently not fused to the shaft of the

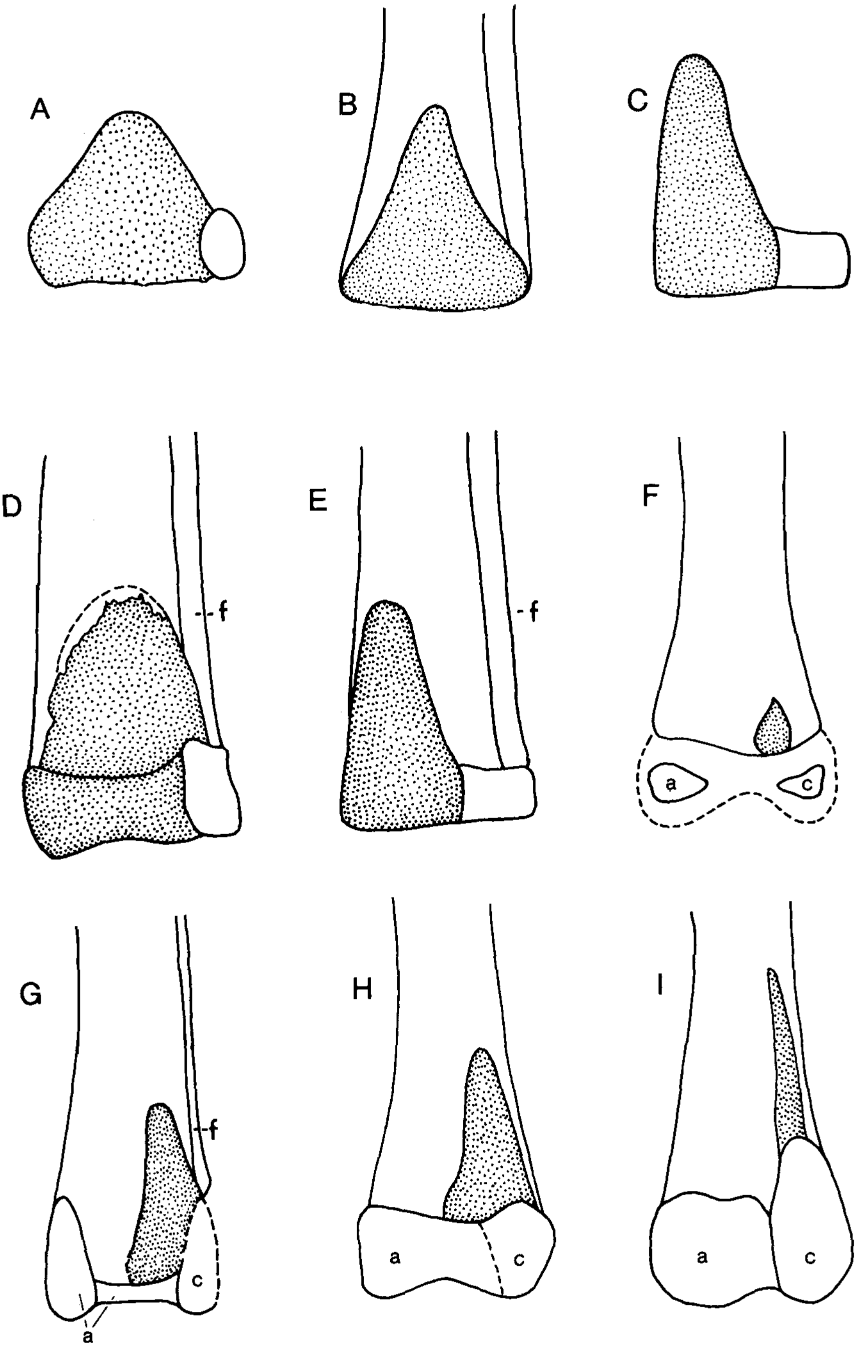

Fig. 1. Tibia and tarsus of dinosaurs and birds. (A–C) Various restorations of the tarsal region in *Archaeopteryx* (after Ostrom 1976a, Figs. 28f, 29c, 31e); (D) the theropod dinosaur, *Deinonychus*; (E) *Archaeopteryx* as described and illustrated by Ostrom (1976a), a combination of B and C above; (F) the domestic chicken, *Gallus* (after Jollie 1977); (G) *Archaeopteryx* restored after the London, Berlin, and Eichstätt examples; (H) *Baptornis advenus*; (I) the hoatzin, *Opisthocomus hoazin,* after Parker (1891). The coarsely stippled area represents the so-called "ascending process." Abbreviations: f = fibula, a = astragalus, c = calcaneum.

tibia. The ankle joint is of the mesotarsal type, with movement occurring between the proximal and distal tarsals. Although the presence of this type of mesotarsal joint has been used to unite birds and dinosaurs, the homologies of the tarsal bones making up the joint have never been clear. Part of the problem is caused by the reduction of the fibula, which, in birds, rarely reaches distally more than three-fourths of the length of the tibia. Even in *Archaeopteryx,* the fibula terminates above the level of the tarsals that form the joint. This means that the most lateral of the proximal tarsal elements must underlie the outer margin of the tibia rather than the fibula. This lateral tarsal element forms the outer condyle of the distal end of the tibiotarsus in *Archaeopteryx* and all other birds. It is formed, embryologically, by the fusion of two cartilage elements—the fibulare and a distal centrale (Holmgren 1933). The rest of the distal end of the tibiotarsus, including the outer condyle, is formed by a larger bone comprising the fused intermedium, proximal centrale, and distal centrale (Holmgren 1933). The distal end of the tibiotarsus of a bird is thus composed, at one stage of development, of a small, lateral calcaneum (composite "fibulare") and a large, medial astragalus (composite "tibiale," Fig. 1F). In this respect the mesotarsal joint of birds compares well with that of other advanced, bipedal archosaurs (ornithopods and theropods).

Just above the tarsus of *Archaeopteryx,* a thin sheet of bone is closely appressed to the tibial shaft. Ostrom has described this bone as an "ascending process of the astragalus" and homologized it with a corresponding structure in the theropod ankle. Although there has been some recent speculation that this process is a calcite deposit on the *Archaeopteryx* slabs, there can be little doubt that this structure is bone (it glows under ultraviolet light, while the calcite does not) and that it is present in the same position in at least the London, Berlin, and Eichstätt specimens. In modern birds this process appears rather late in development, after the fusion of the proximal tarsals, as a long triangular cartilage in front of the lateral side of the distal end of the tibia and just above the calcaneum (Fig. 1F, I). After ossification, it fuses with the proximal tarsus, the distal end of the tibiotarsus. A brief description of this bone is given by Morse (1872: 12–16) and Wyman (*in* Morse 1872: 11–12), who termed it the "pretibial" bone. Subsequent workers, familiar with the similar structure in dinosaurs, termed it the "astragalar process" (Baur 1883; Osborn 1900; Heilman 1926; Ostrom 1975a, 1976a).

We think that the pretibial bone of birds and the ascending process of the theropod dinosaur astragalus are nonhomologous. In theropods the process is a broad extension of the astragalus, which covers much of the anterior face of the tibia (Fig. 1D). In contrast, the pretibial bone of birds is a separate ossification on the lateral side of the tibia. When it fuses to a joint-forming tarsal, it always fuses to the calcaneum (outer condyle), although some contact may be made with the more medial astragalus. It is the last tarsal cartilage to appear in the developing embryo. The pretibial bone can be clearly seen in the tibiotarsus of the Lower Cretaceous *Enaliornis* (where it may not completely fuse to the tibia, even in adults) and in the Upper Cretaceous toothed birds *Hesperornis* and *Baptornis* (Fig. 1H). In these birds, in contrast to the astragalus of theropod dinosaurs, it is a high, narrow ossification associated primarily with the calcaneum. These differences in placement and its late appearance during development suggest that it is a uniquely derived character for birds and is properly termed a pretibial bone, rather than an astragalar process.

Ostrom (1976a) has described the tarsus of *Archaeopteryx* as identical with that of a theropod dinosaur, although his restorations of this region vary substantially

(Fig. 1A–C). To facilitate comparisons, we have combined his figures and verbal descriptions in our Fig. 1E, which utilizes his clearest restoration of the astragalus and calcaneum. Regardless of which restoration is used, his description of the tarsus is essentially that of a theropod, having a small lateral calcaneum underlying the fibula and with a large astragalus extending up the middle of the tibial shaft (Fig. 1E). This morphology would be unlike that of any other Mesozoic or any modern bird. We have re-examined all of the specimens of *Archaeopteryx* that show the tarsals, and it is clear that the fibula has a distal connection with the lateral border of the tibia rather than with the calcaneum. The so-called "ascending process" is on the extreme lateral side of the tibia, primarily associated with the calcaneum as in all other Mesozoic birds (Fig. 1G). In other words, the "ascending process" of the *Archaeopteryx* ankle is a pretibial bone of the avian type. The extreme lateral position of the pretibial bone is clearly visible in Ostrom's (1976a, Fig. 17) photographs of the Berlin and London specimens.

MORPHOLOGY OF AVIAN DENTITIONS

Sir John Evans (1865) first noted the presence of teeth in a Mesozoic bird (*Archaeopteryx*), but his report had been largely ignored (Gingerich 1976). Twelve years elapsed before a second specimen proved that *Archaeopteryx* indeed bore teeth (Giebel 1877). The accounts of Marsh (1873, 1875), describing the toothed forms from the Upper Cretaceous of Kansas, comprised the first widely accepted proof of teeth in early birds. This was very important in establishing the reptilian origin of birds. Marsh noted differences between the morphology, mode of implantation, and mode of replacement of the teeth of the two genera, *Hesperornis* and *Ichthyornis*. He reported (1875, 1880) that *Ichthyornis* possessed teeth in distinct sockets and maintained (1880: 125) that tooth replacement takes place "vertically as in the crocodiles and dinosaurs." Conversely, he observed that the dentition of *Hesperornis* is set in slightly constricted grooves and is replaced "laterally" as in the mosasaurs. He stated that the teeth of *Hesperornis,* like those of mosasaurs, have expanded roots and that they resemble those of mosasaurs more than those of *Ichthyornis* (Marsh 1875, 1880). To this, Gregory (1952) only added that the interalveolar septa were somewhat thinner than Marsh indicated. He also expected to see expanded bony roots on the teeth assigned to *Ichthyornis,* but this is partially explained by his belief at the time that these actually were from mosasaurs.

Through the use of radiographs, Martin and Stewart (1977) confirmed that the roots of the dentition of *Ichthyornis* are expanded, as in Marsh's illustrations of *Hesperornis* teeth, and that the teeth of these two genera are more similar to one another than either is to the teeth of mosasaurs. They also described a specimen of *Ichthyornis* in which the mandibular dentition is set in a continuous groove, as in young crocodilians and *Hesperornis,* and ascribed this condition to the subadult nature of the specimen. (Some mandibular sutures not visible in other *Ichthyornis* specimens are still visible). They also hypothesized that this type of implantation in adult *Hesperornis* might be neotenic.

Evans (1865) described the teeth of *Archaeopteryx* as consisting of a slightly tapered, flattened enamel crown set upon a wider, semi-elliptical bony base. This description was based upon the British Museum specimen in which the maxilla is split open. All other specimens conceal the nature of the root. Although the excellent ultra-violet photograph of deBeer (1954, P. IX, Fig. 4) illustrates the resorption pits

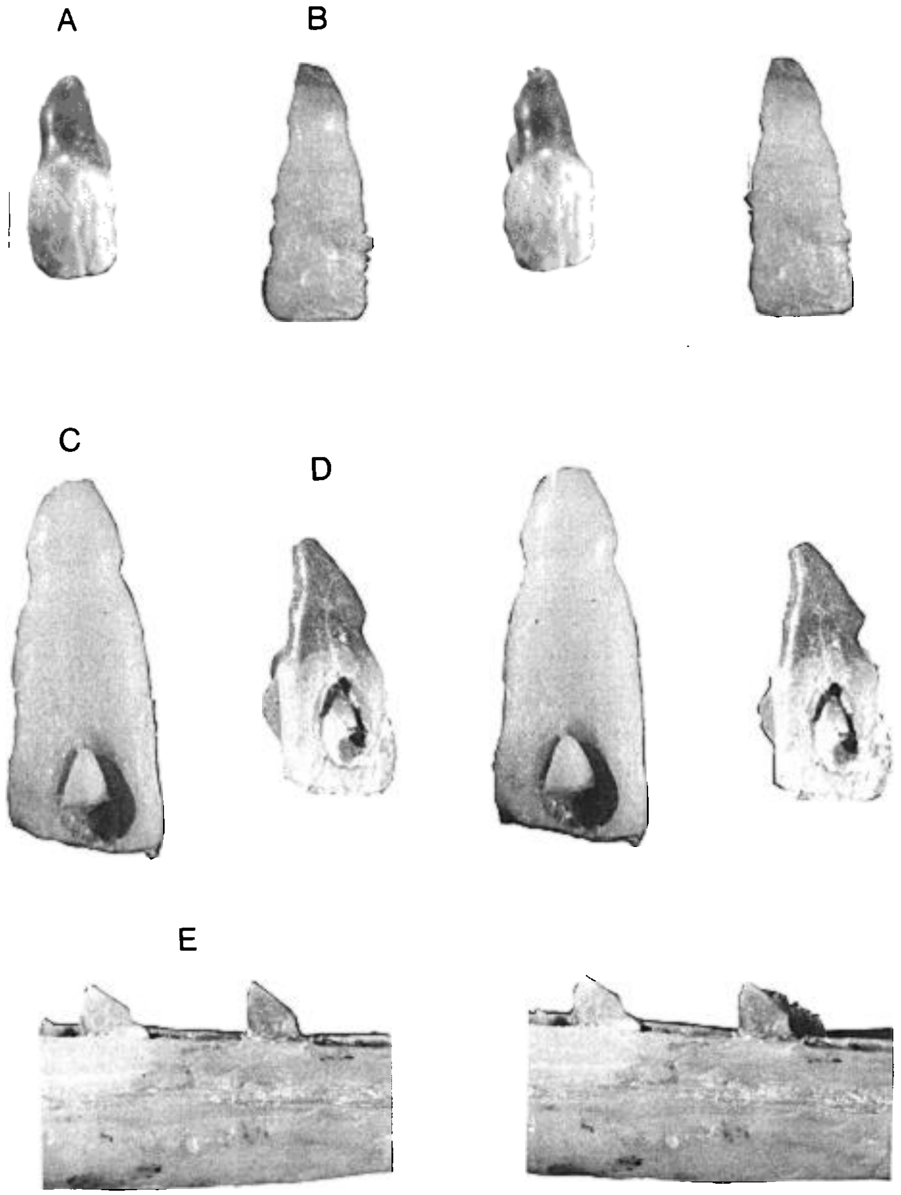

Fig. 2. Stereophotographs of teeth of birds and crocodiles. (A) Lateral view of tooth of a hesperornithid [University of Kansas Vertebrate Paleontology (KUVP) 2287]; (B) lateral view of tooth of recent *Alligator mississippiensis*; (C) medial view of tooth of *A. mississippiensis* undergoing replacement; (D) medial view of tooth of hesperornithid (KUVP 2287) undergoing replacement; (E) lateral view of right mandible of *Ichthyornis victor* (Sternberg Memorial Museum 13520) showing constriction and expanded bony base of teeth.

on the lingual sides of the teeth of the maxilla, he never mentioned them. But Edmond (1960) noted that these resorption pits in the barrel-like bases of the teeth of *Archaeopteryx* are reminiscent of the manner in which crocodiles replace their teeth (i.e. the embryonic tooth develops in association with a pit in the lingual side of the root of the predecessor, and the replacement tooth enters the pulp cavity and eventually expels the old tooth). Furthermore, in both *Hesperornis* and *Archaeopteryx,* the replacement tooth develops in an oval to circular resorption pit in the linqual side of the root of the tooth being replaced. This probably is also the condition in *Ichthyornis,* although no exposed tooth bases are known for the genus. Additionally, both *Ichthyornis* and *Hesperornis* have teeth set in a constricted groove, at least in the juvenile state. This feature has never been recorded in *Archaeopteryx,* but this might be because all of the specimens are adults. In all of the known toothed birds, the teeth are laterally compressed and unserrated. The triangular crowns are separated from the expanded roots by a distinct waist. Because these dental features appear to be primitive for birds, one might reasonably expect to see them exhibited by the archosaurian group to which birds are most closely related. We think that the closest approach to an avian type of dentition is found in the Crocodilia.

All of the extant crocodilians have teeth of the avian type, at least in subadult stages, and especially in the posterior part of the jaws. Although teeth of larger individuals tend to be conical and to show less constriction, the teeth of juvenile alligators, gavials, and caimans clearly show a laterally compressed crown usually separated from an expanded bony root by a definite constriction. The replacement tooth develops in a roughly circular resorption pit in the lingual side of the base of its predecessor and enters the pulp cavity. All but the anterior teeth of juvenile crocodiles and alligators are set in a slightly constricted groove. Interdental septa form from front to back, just as in *Ichthyornis.* The similarity of alligator and bird teeth is striking. Figure 2 compares hesperornithid teeth with teeth of *Alligator mississippiensis.*

This basic type of tooth is widely distributed within the fossil Mesosuchia and Eusuchia. Although the teeth of proterosuchians are poorly known, Nash (1971) has described the teeth of the Triassic *Orthosuchus* as being conical and unserrated. After the Triassic only sebecosuchian and pristichampsid crocodilians have serrated teeth (Langston 1973).

Theropod dinosaurs, by comparison, have serrated teeth with straight roots and no constriction. The mode of tooth replacement is essentially like that of birds and crocodiles, although the resorption pits tend to be elongate (Edmund 1960). Although the details of tooth replacement are not available for primitive archosaurs, early archosaurs of the proterosuchian and pseudosuchian grades apparently have teeth of the theropod type. Serrated teeth with straight roots and no constriction (so far as the dentition is visible in the specimens) are known in *Chasmatosuchus, Ankistrodon, Saurosuchus, Shansisuchus, Euparkeria, Hesperosuchus, "Mandasuchus," Wangisuchus, Platyognathus, Sphenosuchus,* and *Erythrochampsa.* This morphology is apparently primitive for archosaurs and the avian/crocodile condition can be assumed to be derived.

SUMMARY AND CONCLUSIONS

Ostrom (1975a, 1976a) has stated that the skeleton of *Archaeopteryx* is essentially identical with that of some small theropod dinosaurs: "Were it not for those remarkable feather imprints, today both specimens would be identified unquestionably as coelurosaurian theropods" (Ostrom 1976a: 109). We think that many of these "coelurosaurian" features are incorrectly identified. This is certainly true of the tarsal region, where *Archaeopteryx* has a pretibial bone, fibula, and calcaneum of the avian type. In the dentition, *Archaeopteryx* has unserrated teeth with constricted bases and expanded roots like those of other Mesozoic birds. This latter, derived feature is also shared by most fossil and recent crocodilians. The dental structure provides additional support for Walker's (1972) hypothesis of a "sister group" relationship between birds and crocodiles, with both groups sharing a common pseudosuchian origin.

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