

## A NEW FAMILY OF BIRD-LIKE DINOSAURS LINKING LAURASIA AND GONDWANALAND

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**ABSTRACT**—A new family of theropod dinosaurs is described based on metatarsi from North America and Argentina. Because birds are theropod descendants, there are often problems in assigning isolated metatarsi to the proper group. Differences between the metatarsi of ground birds and theropods are detailed. In particular, it is shown that the length/width ratio of articulated metatarsi cannot be used to distinguish higher taxa. This new family represents the first occurrence of the same genus of theropod dinosaur from both Laurasia and Gondwanaland at the end of the Cretaceous, a time when the two supercontinents were supposedly still separate.

### INTRODUCTION

In 1975, an expedition from the University of California (Berkeley) collecting in the Hell Creek Formation (Cretaceous, Maastrichtian) of Montana, recovered fragments of fossil bird bones associated with dinosaurian and other reptilian remains. This collection included a complete metatarsus (UCMP 117600, Fig. 3A-I) that was called dinosaurian by neoornithologists but avian by most dinosaur paleontologists! The question then arose as to how to separate the metatarsi of dinosaurs morphologically from those of birds. While pursuing this problem, the authors examined the material from the Lecho Formation (Cretaceous, Maastrichtian?) of Argentina, at that time on loan to the University of Florida and to the British Museum (Natural History) in London. This material (with the exception of a metatarsus on loan to the University of Florida), was recently described as a new subclass of birds (Walker, 1981), the Enantiornithes. In this unassociated and mixed assemblage are two metatarsi (Figs. 2K-L, 3J-P) that closely resemble, and share derived characters with, the metatarsus from Montana (UCMP 117600) described here. These metatarsi mark the first occurrence of the same Cretaceous dinosaur genus from both Laurasia and Gondwanaland at the end of the Mesozoic, a time when the two supercontinents were supposedly still separate (Kauffman, 1977; Rage, 1981). This supports an earlier hypothesis (Brett-Surman, 1979) of a land connection between North and South America based on the paleobiogeography of hadrosaurs and ceratopsians (Reptilia; Ornithischia).

**Institutional Abbreviations**—BMNH = British Museum (Natural History), London; HMN = Humboldt Museum, Berlin; JM = Jura Museum, Eichstätt; PU = Princeton University; UCMP = University of California

(Berkeley); UNT = Universidad Nacional de Tucumán.

### THEROPOD AND BIRD METATARSIS

A series of studies conclusively demonstrates that theropod dinosaurs and birds have an ancestor-descendant relationship (Ostrom, 1974, 1976; Bakker and Galton, 1974; Bakker, 1975; Osmólska, 1981; Padian, 1982; Paul, 1984; Benton, 1984; Paul and Carpenter, unpublished). As a consequence, there is considerable morphological similarity and parallel evolution between the two clades. In particular, there often are problems in assigning isolated theropod or bird-like metatarsi, such as those discussed herein, to the proper group.

Traditionally, two characteristics used to separate birds from theropods are the length/width (L/W) ratio of the metatarsus and the degree of fusion of the metatarsus. As an example, *Sagittarius* (the Secretary bird) has a L/W ratio of 31/1 while *Allosaurus* (a Jurassic theropod) has a L/W ratio of only 2.5/1. Figure 1 shows that the overlap of the two clades (birds and theropods) is almost total for animals with a metatarsus longer than 80 mm, based on a sample of 31 families of dinosaurs and birds. Consequently, the length/width ratio of the metatarsus can no longer be considered a valid criterion for separating birds from theropods and other dinosaurs. It must be emphasized that in the fossil record, size alone cannot be used to distinguish taxa without reference to actual structural and morphological features.

Birds have a fused metatarsus while that of theropods is typically unfused. Fusion of this element, or a less extensive coossification, is known to occur in the theropods *Ceratosaurus* (Gilmore, 1920), *Coelophysis* (Raath, 1969, =*Syntarsus*, Paul, 1984), *Elmisaurus*



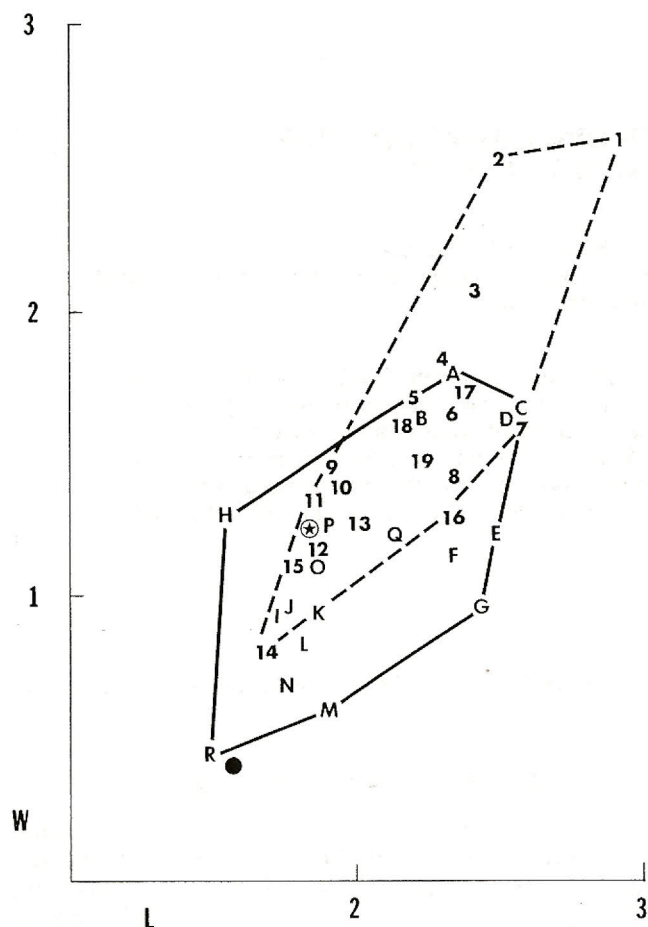


FIGURE 1. A log-log scale of the length (X-axis) versus the midshaft diameter or width (Y-axis) of metatarsi in natural articulation. Integers on the axes are powers of 10 measured in millimeters. Numbers refer to bipedal dinosaurs and letters refer to birds.  $\odot$  = *Avisaurus*,  $\bullet$  = *Dipus* (Rodentia, Mammalia). Dinosaurs: 1 = *Tyrannosaurus*, 2 = *Allosaurus*, 3 = *Ceratosaurus*, 4 + 7 = *Ornithomimus*, 5 + 11 = *Dryosaurus*, 6 = *Ornitholestes*, 8 = *Gallimimus*, 9 = *Hypsilophodon*, 10 = *Nanosaurus*, 12 = *Laosaurus*, 13 = *Coelophysis*, 14 = *Archaeopteryx* (postcranially a dinosaur; based on BMNH 37001, HMN MB.1880/81.4598), 15 = *Compsognathus*, 16 = *Struthiomimus*, 17 = *Macrophalangia*, 18 = *Velociraptor*, 19 = *Elmisaurus*. Birds: A = *Pachyornis*, B = *Diornis* (juvenile), C = *Diatryma*, D = *Diornis* (adult), E = *Rhea*, F = *Dromaeus*, G = *Sagittarius*, H = *Pygoscelis*, I = *Pandion*, J = *Sula*, K = *Apteryx* (juvenile), L = *Falco*, M = *Aramides*, N = *Opisthocomus*, O = *Apteryx* (juvenile), P = *Apteryx* (adult), Q = *Hesperornis*, R = *Ichthyornis*. The regression equation for both birds and dinosaurs, excluding the penguin, is  $Y = 1.06X - 0.92$  and where  $r = 0.8$ .

(Osmólska, 1981), and in *Archaeopteryx* (Ostrom, 1976). Possible occurrences have also been reported in *Avipes* (Von Huene, 1932) and in *Heterodontosaurus* (Santa Luca, 1980). Indeed, metatarsal fusion is typical of gracile ungulates, and is also known in a rodent (Rich, 1973). Fusion or coossification in dinosaurs and

TABLE 1. Characteristics of metatarsi that separate birds and dinosaurs.

Birds	Dinosaurs
1) Metatarsal fusion distal at first, then proceeds proximally; metatarsal bundle fusion complete.	1) Fusion rare, restricted to proximal end; bundle coossification rare; complete bundle fusion absent.
2) Metatarsal III proximally pinched, not visible in anterior view at proximal end.	2) Often proximally pinched and visible over entire length.
3) Foramen present between metatarsals III & IV.	3) No such foramen.
4) Distal tarsals always completely fused to metatarsals in adults.	4) Complete fusion absent, except in <i>Elmisaurus</i> .
5) Hypotarsus very prominent, developed behind metatarsal III (except <i>Hesperornis</i> ).	5) Hypotarsus moderately developed behind metatarsals II & III.

in *Archaeopteryx* is more closely related to age and health. In *Elmisaurus*, it may be the normal condition (Osmólska, 1981).

Table 1 lists five characteristics of metatarsi. Each characteristic may occur in both groups with varying degrees of frequency, but taken as two "character suites," they reliably separate the metatarsi of theropods from those of post-*Archaeopteryx* birds.

Theropod and avian metatarsi represent an excellent example of both the similarities and the differences that can be found within an ancestor-descendant relationship. The similarities include a laterally compressed, tridactyl pes in which metatarsal I no longer articulates with the ankle, digit I is a semi-reversed hallux, and metatarsal V is either extremely reduced or lost. This adaptive suite is not found in any other tetrapod clade and may have evolved only once. As such, it is an excellent minimum definition of the theropod-bird clade.

The differences, however, are also important. In birds, fusion of the metatarsal bundle starts distally and migrates proximally with ontogeny (Fig. 2). In theropods, the coossification is always more pronounced proximally (Fig. 2). This is also the case in the Montana and Argentina metatarsi (Fig. 3). Note that metatarsal fusion/coossification in theropods occurs erratically, being found in some, but not all, basal and derived taxa. Almost all birds (except for some psittacids and spheniscids) including *Hesperornis* and *Ichthyornis*, have a metatarsal III that is proximally pinched and hidden behind metatarsals II + IV. Varying degrees of proximal and lateral compression (pinching) of metatarsal III is a derived feature found in the theropod dinosaurs most closely linked to bird



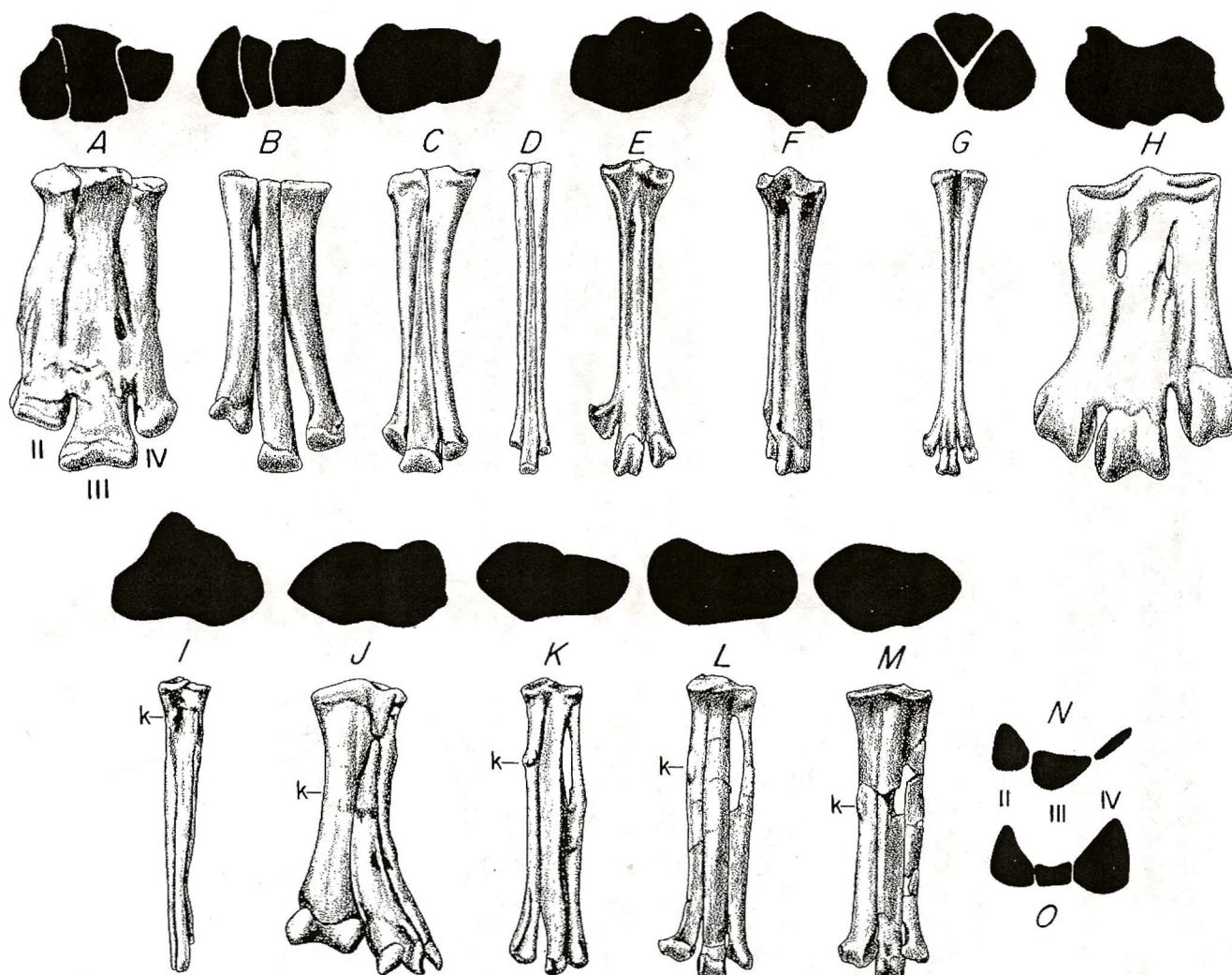


FIGURE 2. Left metatarsi of dinosaurs and birds in anterior view (shaded) and proximal view (black). A, *Ceratosaurus*; B, *Velociraptor*; C, *Elmisaurus*; D, *Archaeopteryx* (based on BMNH 37001, HMN MB.1880/81.4598); E, *Ichthyornis*; F, *Hesperornis*; G, *Rhea* (juvenile); H, *Pygoscelis*; I, "Enantiornithes," UNT 4021; J, "Enantiornithes," UNT 4053; K, *Avisaurid* UNT 4048; L, *Avisaurus* sp., UNT uncataloged specimen; M, *Avisaurus archibaldi* (holotype); N, midshaft cross-section of *Avisaurus archibaldi*; O, midshaft cross-section of *Elmisaurus*. Knob for proposed origin of m. tibialis anticus = k. Figures 2 and 3 by the junior author.

ancestry (Paul, 1984), and in true birds. Examination of *Archaeopteryx* (BMNH 37001, JM SoS 2257) shows a moderate degree of proximal compression of metatarsal III (contra Ostrom, 1976). The Montana and Argentina metatarsi contrast in having a proximally robust metatarsal III, a condition found elsewhere in such basal theropods as *Coelophysis* (= *Syntarsus*) and *Ceratosaurus*. The avian hypotarsus is usually a well developed proximal-posterior projection encompassing all three metatarsals. It is smaller and more medial in theropods and *Archaeopteryx* (compare proximal views of Fig. 2A–C with 2E–G). This latter condition is found in the Montana and Argentina metatarsi.

It should be noted that the metatarsus of *Archaeopteryx* is of the fully theropod type according to all of

the above criteria. However, it is beyond the scope of this paper to settle the higher systematics of *Archaeopteryx* only on the basis of its metatarsus.

It is readily apparent that the Argentina and Montana metatarsi are more like those of theropods than of birds. It is possible that these metatarsi are those of enantiornithids, and that the enantiornithids represent a sister group to other birds that retain a theropod-like foot. The Argentina and Montana metatarsi, however, are morphologically distinct from the described enantiornithid metatarsus (UNT 4053, Walker, 1981). Because the metatarsi figured here are more like those of theropods, it is best to place them in the Theropoda. We emphasize that our placement of these particular metatarsi in the Theropoda does not affect the place-



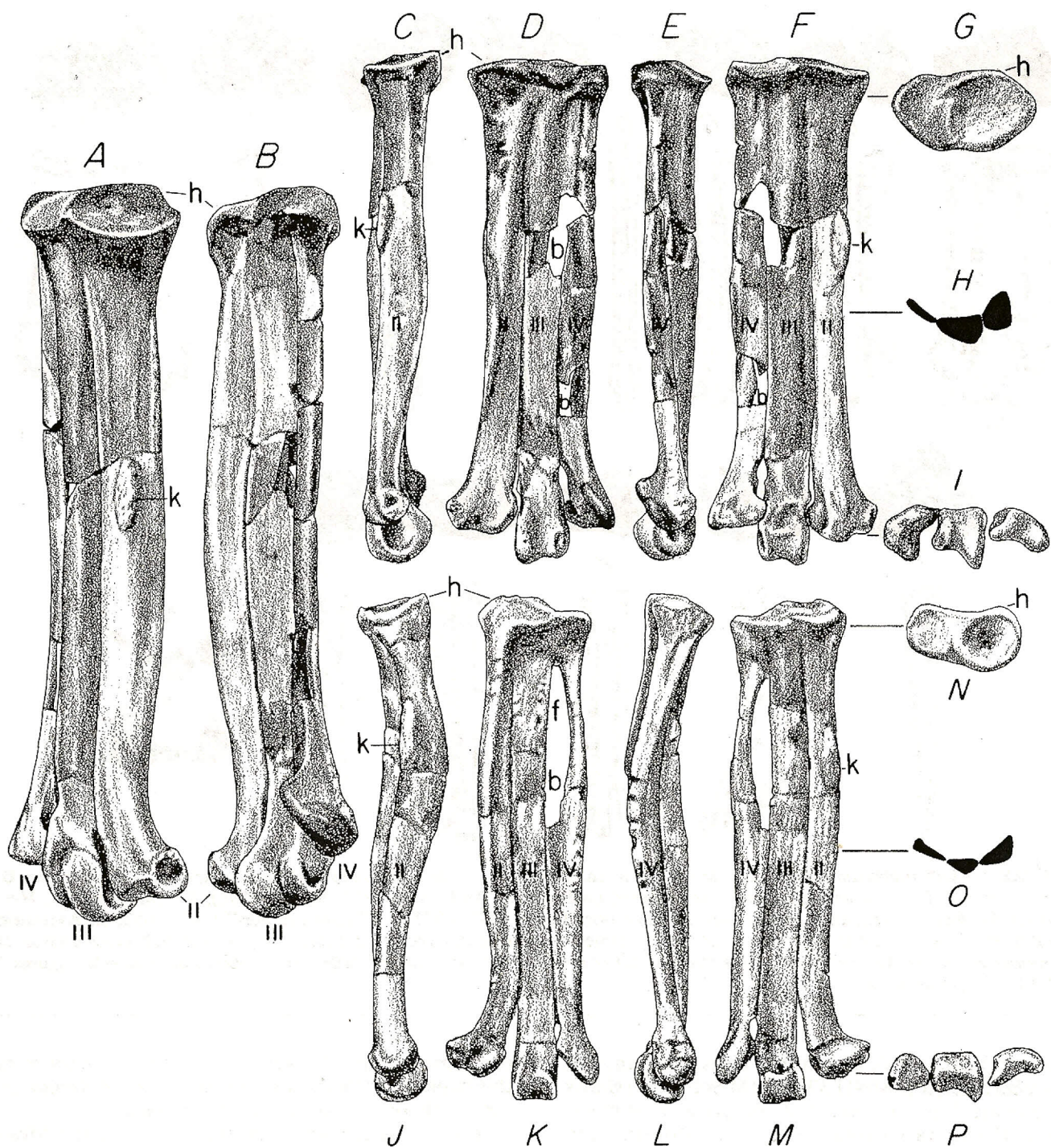


FIGURE 3. A-I, right metatarsus of *Avisaurus archibaldi*, holotype, UCMP 117600. A, anterior view; B, posterior oblique view; C, medial view; D, posterior view; E, lateral view; F, anterior view; G, proximal view; H, cross-section; I, distal view. J-P, left (reversed) metatarsus of *Avisaurus* sp. from the Lecho Formation of Argentina, UNT uncataloged specimen. J, medial view; K, posterior view; L, lateral view; M, anterior view; N, proximal view; O, cross-section; P, distal view. Hypotarsus = h; knob for proposed origin of m. tibialis anticus = k; possible fenestra = f; postmortem breakage = b. Maximum length of UCMP specimen is 75 mm. Maximum length of referred UNT specimen is 47.5 mm.



ment of the other Lecho material by Walker (1981) in the Enantiornithes. The uniquely divergent morphology of the theropod-like metatarsi easily justifies a new taxon at the family level.

## SYSTEMATIC PALEONTOLOGY

Class ARCHOSAURIA  
(sensu Bakker, 1975; Cooper, 1981)  
Order SAURISCHIA  
Suborder THEROPODA  
Family AVISAURIDAE, new family  
Genus AVISAURUS, new genus

AVISAURUS ARCHIBALDI, new species

**Holotype**—UCMP 117600, left metatarsus, collected in 1975 by the University of California Museum of Paleontology.

**Paratypes**—Small right metatarsus from the Lecho Formation of Argentina [uncataloged, Fig. 3J-P]; UNT 4048, originally described by Walker, 1981, and refigured here (Fig. 2K); PU 17324, isolated right metatarsus from the Hell Creek Formation, Montana.

**Horizon**—Hell Creek Formation, Cretaceous, Maastriichtian, UCMP locality V73097, Garfield County, Montana, U.S.A.

**Etymology**—Literally "bird-lizard" (a deliberate mixture of Latin and Greek to emphasize the archosaurian-avian nature of this genus). Species after J. David Archibald, its discoverer.

**Diagnosis**—Diagnosis of family and genus same as for species. Metatarsal III visible in anterior view over its entire length and is the broadest element proximally; metatarsals II + IV equal in length with large, medial, concave articular facets proximally; metatarsal IV trochlea vestigial, highly divergent, spoon shaped and asymmetrical; knob on metatarsal II (for insertion of the m. tibialis anticus?) relatively larger than in any other theropod; metatarsus very strongly lunate in cross-section and concave posteriorly; metatarsal IV shaft a flat strap; metatarsal III triangular in cross-section; metatarsal II the most robust; tendency for metatarsus to be coossified into a pseudo-tarsometatarsus; fusion only at proximal end.

**Comments**—The paratype Lecho material may prove to be distinct at the species level in the bending of the metatarsal shafts, the presence of a possible fenestra between metatarsals III and IV, the more divergent angle of metatarsal II from metatarsal III, the relatively higher position of the insertion for the m. tibialis anticus, and the narrower articular area for the reception of the tibia. Notably, the Princeton specimen (PU 17324), shows the distal ends of the metatarsals were unfused, but proximally it has a very strong rugose suture for metatarsal II.

Having placed *Avisaurus* in the Theropoda, the question arises as to whether it can be placed phylogenetically relative to other theropods. In proportions, and especially in their uncompressed central metatarsal, *Avisaurus* retains the conservative condition seen in

such basal theropods as *Coelophysis* and *Ceratosaurus* (Fig. 2), and thus retains a basal condition compared to derived theropods and *Archaeopteryx*, which have proximally pinched central metatarsi (e.g. compsognathids, ornitholestids, allosaurids, tyrannosaurids, elmisaurids, ornithomimids, dromaeosaurs, and saurornithomimids; Paul, 1984). In contrast, the concave posterior cross-section of the metatarsal bundle is strongly reminiscent of derived theropods, especially *Elmisaurus* (Fig. 2N-O), and to a lesser degree tyrannosaurids, ornithomimids, dromaeosaurs and *Archaeopteryx* (Paul and Carpenter, unpublished). *Avisaurus* shares the coossification of the metatarsal bundle with both basal and derived theropods, and the fusion of the proximal articular facets into a smooth continuous surface with derived theropods. However, *Avisaurus* differs remarkably from all known theropods in that the distal articular facets for the phalanges are very poorly developed, with the second and fourth facets especially underdeveloped and divergent. Indeed, the fourth metatarsal may be on the verge of becoming vestigial resulting in a striking convergence with *Struthio*. Only the third facet is symmetrically developed. *Avisaurus* combines basal and derived theropod characteristics along with unique characteristics of its own. This makes it impossible to ascertain the exact position of *Avisaurus* vis-à-vis other theropod infraorders at this time. This is especially true because we can only consider the metatarsi.

The functional implications of the flattened and lunate cross-section of the *Avisaurus* metatarsus is not clear. The metatarsus of *Avisaurus* does not resemble that of penguins or any other swimming birds (Fig. 2) but is closer to that of ground runners. The anteroposteriorly-flattened metatarsus suggests that they were not especially fast but the unusual development of the m. tibialis anticus attachment surface implies a strong degree of control over the rotational vector while turning. This might have enhanced maneuverability and hence the ability to capture prey.

*Avisaurus* also has paleobiogeographic implications. It is the first Late Cretaceous theropod recorded from both Laurasia and Gondwanaland. In addition to the presence of the fully terrestrial hadrosaurs and ceratopsians, the presence of avisaurids supports a probable land connection between Laurasia and Gondwanaland during the latest Cretaceous, supposedly a time when a connection did not exist (but see Rage, 1981).

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