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## The Tarsus of the Paleocene Leptictid *Prodiacodon* (Insectivora, Mammalia)

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### INTRODUCTION

The Leptictidae occupy an unusually important position among eutherian mammals. Several unknown Cretaceous members of the family were probably ancestors of the primates, insectivores, and virtually all the known eutherian orders of the Cretaceous and early Tertiary. Most of our knowledge of the Leptictidae is derived from dentitions, and only in the case of the Chadronian *Leptictis* (= *Ictops*, Van Valen, personal communication) have we better than unsatisfactory information about the cranium (Butler, 1956). Sufficient published information on the post-cranial skeleton of the leptictids is virtually non-existent. Brief remarks and inadequate illustrations of the leptictid skeleton can be found in Matthew (1909, 1918, and 1937), based on the fragmentary material available for *Prodiacodon* and *Leptictis*.

The purpose of the present paper is to describe and illustrate the tarsal remains of the dentally most primitive known leptictine, the Torrejonian *Prodiacodon*. It is hoped that detailed information on the early leptictine tarsus will enable workers on Cretaceous mammalian assemblages to identify or to associate the quite common tarsal elements with such important leptictid genera as the procerberine *Procerberus*, recently described by Sloan and Van Valen (1965), and *Gypsonictops*, which is

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the only eutherian species in certain Maestrichtian assemblages. Once tarsal elements are correctly allocated, well-preserved elements of the pelvic limb stand a good chance of being recognized. Extremely valuable potential information is very likely present among the undescribed, miscellaneous "scrap" of most Cretaceous and early Tertiary faunas collected by the screen-washing technique.

I would like to thank Dr. Malcolm C. McKenna, Department of Vertebrate Paleontology of the American Museum of Natural History, for his critical reading of the manuscript. I am indebted to Dr. G. T. Mac Intyre for his constant constructive criticism. I have greatly profited from discussions with Mrs. Sylvia F. Fagan.

### DESCRIPTION AND REMARKS

Several specimens of the American Museum collection of vertebrate fossils contain foot bones of *Prodiacodon*. These specimens are the type of *Prodiacodon puercensis* (A.M.N.H. No. 16011) and A.M.N.H. No. 16748. The best astragalus and a femur of *Prodiacodon* (A.M.N.H. No. 703) were found catalogued with a fragmentary but clearly recognizable lower jaw of *Mixodectes pungens*<sup>1</sup> (A.M.N.H. No. 2451).

### THE ASTRAGALUS

The astragalus consists of two well-defined portions: the proximal body and the distal head. A constricted neck separated the two portions. The body is oriented at an angle of 27 degrees to the longitudinal axis of the neck and head. On the dorsal surface of the body the tibial trochlea is rather deep. The lateral and medial portions of the trochlea are asymmetrical; the deepest point of the trochlea is on the medial half of the body. The fairly high lateral trochlear crest is very sharply

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<sup>1</sup> This controversial specimen has the notoriety of being the subject of two lengthy footnotes. Matthew (1909, p. 547), in a 19-line footnote, meticulously refuted Wortman (1903) who had questioned the association of the postcranial elements with the mandible of *Mixodectes*.

I found that the astragalus (A.M.N.H. No. 703) that was catalogued with the mandible of *Mixodectes* (A.M.N.H. No. 2451) is identical with the astragalus associated with specimens of *Prodiacodon* (A.M.N.H. No. 16011) in its minutest morphological details as well as in size. In addition to the morphological similarity, the astragalus and femur in question are the same creamy-yellow color, whereas the *Mixodectes* mandible is light gray in color, unmistakably different from that of the supposedly associated astragalus. I have no confidence in the possibility that the postcranial elements were associated with *Mixodectes*. Both the astragalus and the femur clearly belonged to a specimen of *Prodiacodon puercensis*.

defined; the medial trochlear crest is equally sharp but somewhat lower. The tibial trochlea narrows down proximally and continues medially for a very short distance onto the ventral surface of the head. The narrow, posterior, and distal fossa of the trochlea is oriented almost exactly in the same direction as the longitudinal axis of the neck and head of the astragalus. The plantar astragalar foramen pierces the body of the astragalus on the ventral side, at the very edge of the trochlea. The blood vessels or nerves, or both, that may have passed through this foramen seem to have run in the interarticular sulcus on the ventral side of the body of the astragalus. The path of the structures, whatever they were, which passed into and very likely also out of the astragalar foramen, appears to have run proximally and then, turning, dorsally in the proximal portion of the body of the astragalus. There is no sign of a superior astragalar foramen.

Ventrally, lateral to the interarticular sulcus, the calcaneo-astragalar facet is concave, large, and shaped like an isosceles triangle, the equal sides being about one and one-half times as long as the base. The acute angle of this triangle is directed laterally about 35 degrees from the longitudinal axis of the body of the astragalus.

The sustentacular facet is roughly tear-shaped. It points in a proximal direction.

The distal naviculocuboid facet covers about 180 degrees in an approximately semicircular configuration. The facet is broadest laterally, and it gradually tapers in a medial, then proximal, direction.

By analogy, the astragalus of *Prodiacodon* is amazingly similar to that of the cat. The orientation and interrelation of the various facets, trochlea, and trochlear crests are very catlike.

## THE CALCANEUM

The best-preserved calcaneum is part of A.M.N.H. No. 16748, although most of the peroneal tubercle is missing. This specimen is about 17 mm. long. The distance from the posterior tip of the astragalocalcaneal facet to the anteriormost point of the cuboid facet is slightly more than half of the length of the calcaneum. The bone is much wider distally than proximally. Proximally, the fossa for the tendon of Achilles is not very pronounced. The internal tuberosity medial to this fossa is more prominent than the external tuberosity lateral to the fossa.

The astragalocalcaneal facet on the dorsal surface faces in a medio-proximal direction; it is almost vertical in relation to the dorsal surface. The angle between the long axis of the calcaneum and the axis of orien-

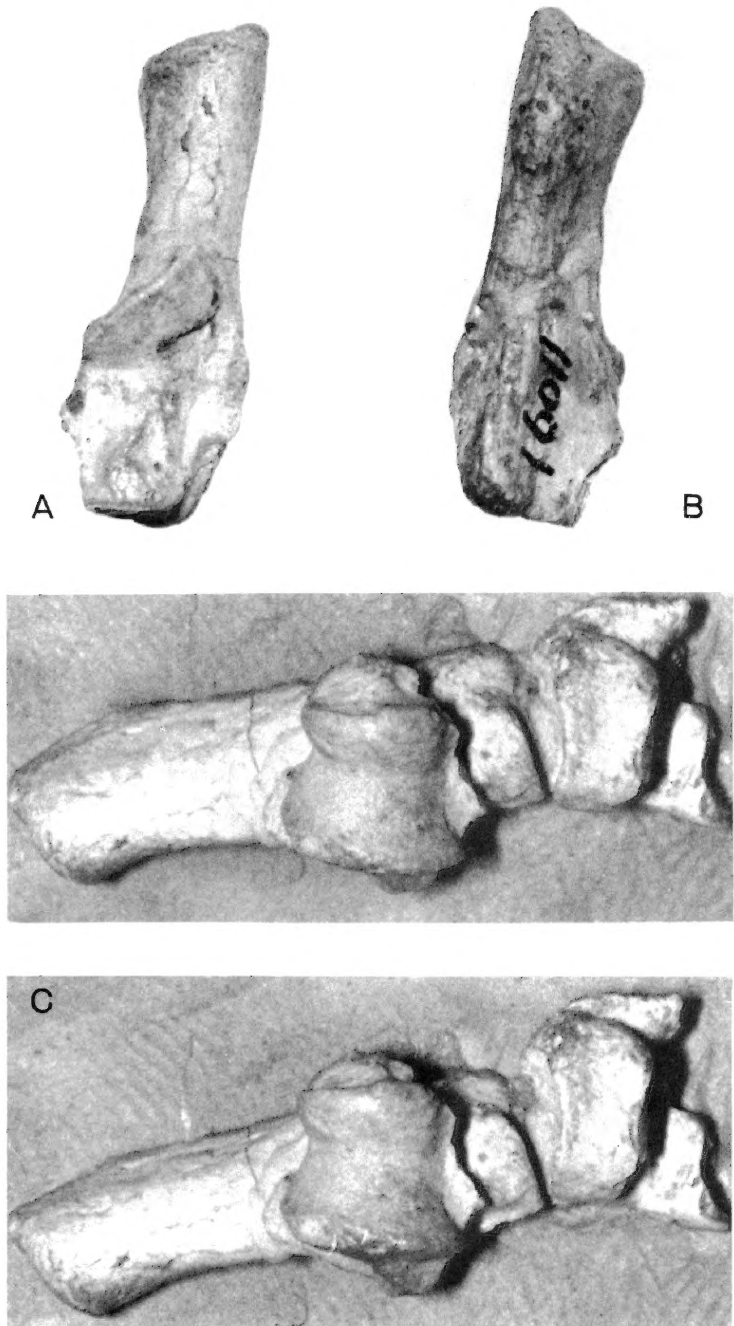


FIG. 1. A, B. Dorsal and ventral views of the calcaneum of *Prodiacodon* (A.M.-N.H. No. 16011). C. Stereophotographs of the incomplete left tarsus of *Prodiacodon* (A.M.N.H. No. 16011); the head of the astragalus is broken off. All  $\times 4$ .

tation of the astragalocalcaneal facet is approximately 40 degrees. This facet is about twice as long as it is wide, and it is slightly convex. Medial and slightly distal to the astragalocalcaneal facet is the sustentaculum. It is slightly concave and irregular in outline. The latter two facets are separated by the interosseous fossa which is a depression in the bone for the interosseous ligament. There is a pronounced pit at the base and lateral to the surface of the sustentaculum. Its function is obscure to me. It may be a depression for the attachment of an annular ligament of the extensor longus digitorum. Distal to the sustentaculum there is a distinct fossa; it probably served to transmit the tendon of the flexor longus digitorum.

The peroneal tubercle is unfortunately broken off both of the known calcanea of *Prodiacodon*. It is clear from what remains that the tubercle extended laterally almost as much as the sustentaculum did medially. On the plantar surface the most prominent is the cuboid facet. The calcaneum of *Prodiacodon* was not in articulation with the navicular. There are no articular facets for this function on either bone.

The distal end of the calcaneum articulated with the proximal surface of the cuboid. Note, however, that on figures 2A and 3A the individual size differences between the various tarsal elements (particularly between the astragali and the calcanea which belonged to different individuals) prevent contact between the calcaneum and the cuboid.

### THE NAVICULAR

The proximal surface, the astragalonavicular facet, which articulates with the astragalus, is shaped like a mediolaterally thickened crescent. There is a ribbon-like, cuboidonavicular, articular facet on the lateral side of the navicular, immediately below the lateral crest of the astragalonavicular facet.

Most of the distal surface is occupied by two very close but distinct articular surfaces. The lateral was probably for articulation with the ectocuneiform; the medial one, with the mesocuneiform. Curiously, on the plantar surface of the navicular, a thick spine extends in a distal rather than a proximal direction. To this spine probably attached the various plantar ligaments.

### THE CUBOID

It is fortunate that the right cuboid can be so well articulated with the corresponding right navicular (both specimens are part of A.M.N.H. No. 16011). Most of the proximal surface articulates with the calcaneum

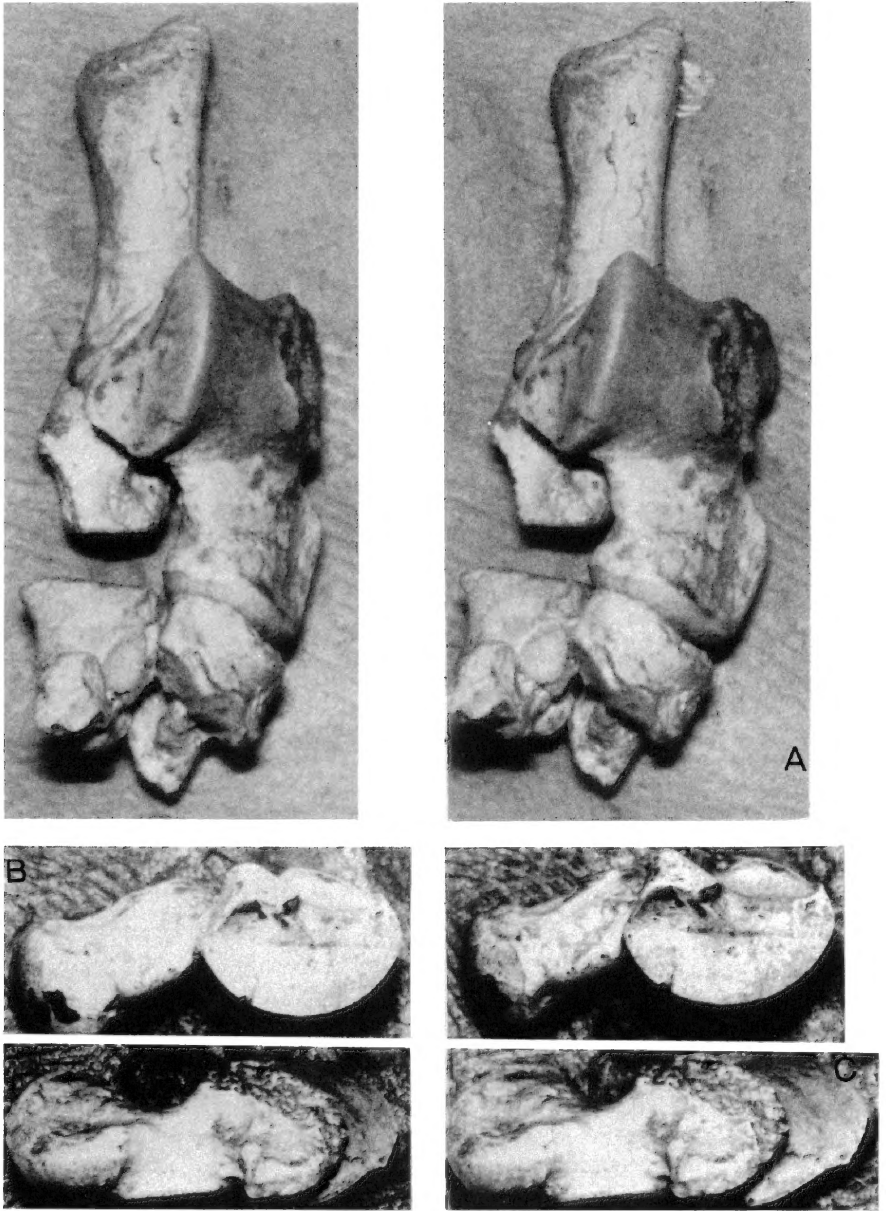


FIG. 2. A. Stereophotographs of composite of left tarsus of *Prodiacodon*; calcaneum, navicular, and cuboid are A.M.N.H. No. 16011, and astragalus is A.M.-N.H. No. 703; dorsal view. B, C. Stereophotographs of astragalus of *Prodiacodon* (A.M.N.H. No. 703) in lateral and medial views, respectively. All  $\times 4$ .

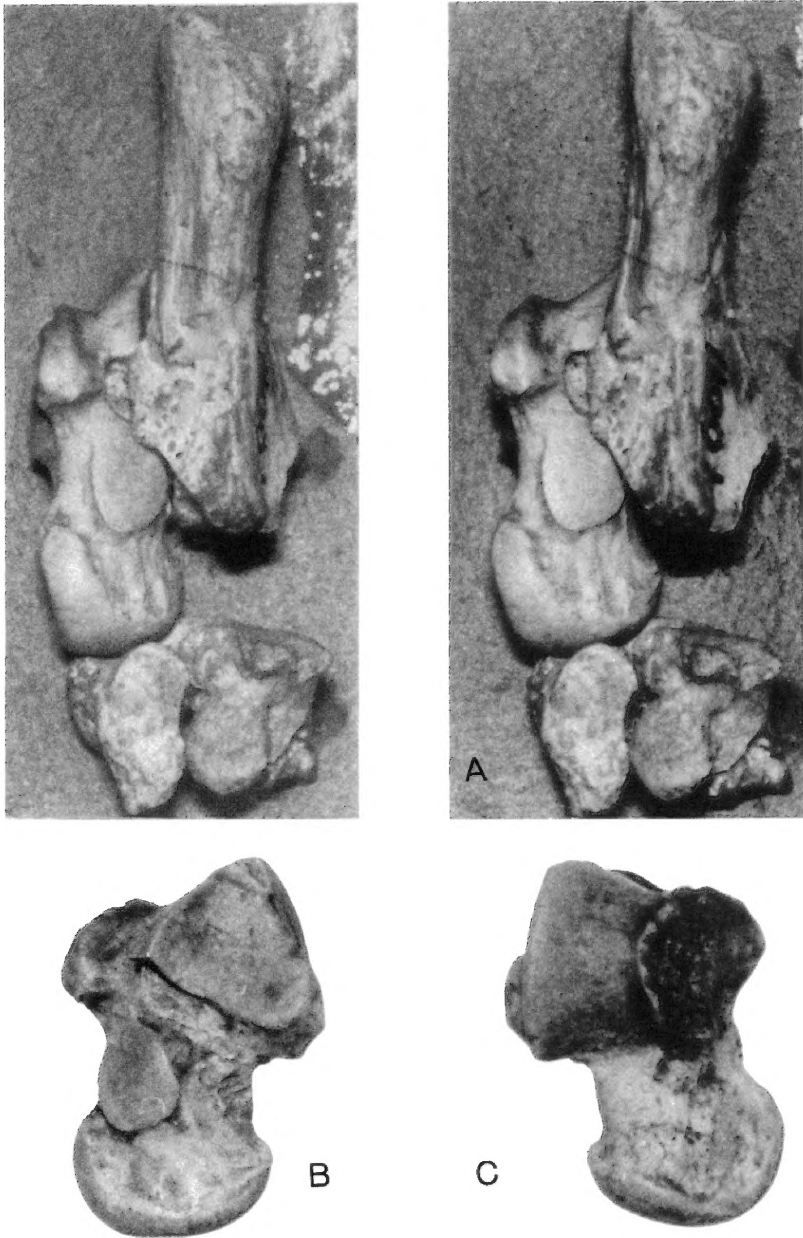


FIG. 3. A. Stereophotographs of composite of left tarsus of *Prodiacodon*; calcaneum, navicular, and cuboid are A.M.N.H. No. 16011, and astragalus is A.M.N.H. No. 703; ventral view. B, C. Ventral and dorsal views of the astragalus of *Prodiacodon* (A.M.N.H. No. 703). All  $\times 4$ .

(the calcaneocuboidal facet) except for a small strip on the medial side, which is the astragalocuboid facet. The two concave facets (the astragalocuboid of the cuboid and the astragalonavicular of the navicular facets) form the basin which accommodates the distal end of the astragalus. The calcaneum is not in contact with the navicular. The naviculocuboid facet is on the medial (or tibial surface) side.

Partly on the fibular surface and partly on the plantar surface of the cuboid there is a very pronounced tuberosity. The proximal portion of the fibular surface is broken off, and the area of the fibular and plantar surfaces that is not occupied by the tuberosity is irregular, having small elevations and depressions for the attachment of ligaments. The distal surface, which is not broken off, was probably an articular surface with the fourth metacarpal. The broken, but important, fibular portion may have provided evidence as to the articulation of the fifth metacarpal with the cuboid. At present we do not know whether *Prodiacodon* had a functional fifth toe or not.

#### THE PECTOCUNEIFORM

Matthew (1918, p. 578) identified this bone (A.M.N.H. No. 16011) as the ectocuneiform. I cannot fully accept such an identification, since the bone is too worn to be correctly identified. Furthermore, the available space distal and between the navicular and cuboid, where the ectocuneiform is expected to fit, makes it very unlikely that the bone in question is the ectocuneiform. It may be the entocuneiform.

#### THE PHALANX

Matthew (1918, p. 578) noted that this bone (A.M.N.H. No. 16011) is of the proximal series. The bone is, however, a second phalanx (it cannot be determined to which of the toes it belonged). It has a spine on its proximal end which articulated on the pulley-like fossa of the distal end of the proximal phalanx.

#### NOTES ON THE ASTRAGALAR FORAMEN

The tarsal bones described in the present paper were closely compared with a fairly well-preserved right astragalus and calcaneum (A.M.N.H. No. 17555) of the leptictid *Diacodon* from the lower beds of the late early Eocene Huerfano Formation of Garcia Canyon region, Colorado. The tarsal remains of the late Wasatchian leptictid show a strong degree of similarity to the Torrejonian *Prodiacodon*.

All previous literature known to me lumps both the foramen on the



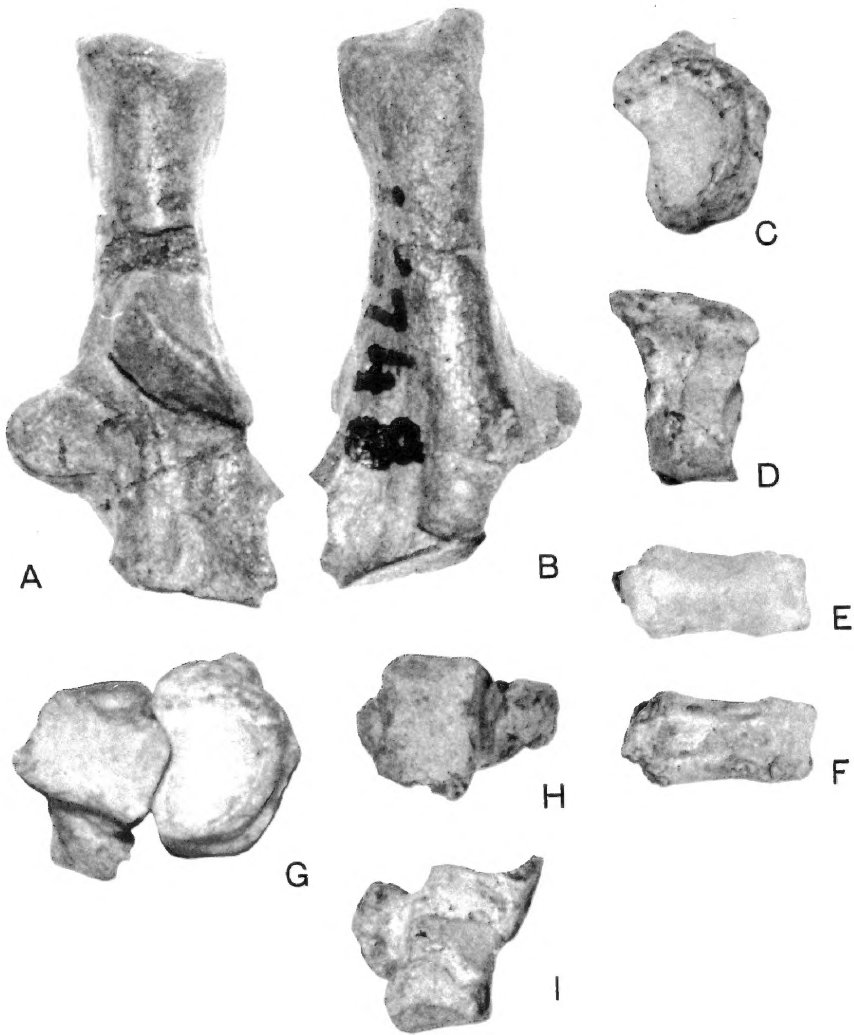


FIG. 4. A, B. Dorsal and ventral views of the calcaneum of *Prodiacodon* (A.M.N.H. No. 16748). C, D. Dorsal (proximal) and lateral views of the navicular of *Prodiacodon* (A.M.N.H. No. 16011). E, F. Dorsal and ventral views of a second phalanx of *Prodiacodon* (A.M.N.H. No. 16011). G. Dorsal view of the cuboid (left) and navicular in articulation (A.M.N.H. No. 16011). H, I. Dorsal and medial views of the cuboid of *Prodiacodon* (A.M.N.H. No. 16011). All  $\times 4$ .

trochlear facet of the astragalus and the one on the plantar surface as astragalar foramina. There is no recognition of a condition, as seen in *Prodiacodon*, in which one foramen can exist without the other.

I propose to name the foramen on the trochlear facet, traditionally referred to as the astragalar foramen, the "superior astragalar foramen,"

and the foramen on the plantar surface of the body of the astragalus at the posterior end of the interarticular sulcus as the "plantar astragalal foramen." There is no doubt that there existed a functional relationship between the superior foramen and the plantar foramen when both were present, i.e., they were the openings at both ends of the canal named here as the "astragalal canal." The well-preserved astragalus of the type (A.-M.N.H. No. 3268) of the Torrejonian arctocyonid *Cleanodon ferox* clearly shows the uninterrupted passage of the astragalal canal from a large and distinct superior astragalal foramen to the equally prominent plantar astragalal foramen.

Schaeffer (1947) pointed out what has been generally stated, namely, that the astragalal foramen (p. 4) ". . . or whatever passed through it, was responsible for greatly restricted movement in the upper ankle joint." He also noted that the trochlear articular surface in the living tubulidentate *Orycteropus*, which has an astragalal foramen, extends posteriorly on both sides of the foramen. He further noted that in the adult *Orycteropus* only some connective tissue was found traversing the canal, without any signs of degenerate blood vessels or nervous tissue. Schaeffer implied that the astragalal foramen, or rather the structures it housed, must have been a restrictive factor during plantar flexion, during which the tibia completely covered the foramen.

The apparent non-function of the astragalal foramina and canal (all of enormous size; see A.M.N.H. No. 51235) in recent *Orycteropus* does not mean there was no original function performed by them. It cannot be supposed, either, that the astragalal canal was non-functional when the superior astragalal foramen was not present. Matthew (1909, p. 551) presented both Ameghino's and his views on the function of the foramen (including both foramina and the canal). According to Matthew, Ameghino held that the canal transmitted a branch of the peroneal artery in modern mammals and that it formerly transmitted the tendon of the flexor hallucis. Matthew did not think that a tendon was ever functionally connected with the astragalal foramen, but fully supported the notion that blood vessels were transmitted through the canal. I believe Matthew was right, although the subject merits further analysis.

In the following discussion the premise is held that the astragalal canal accommodated blood vessels and possibly nerves. Furthermore, I think that the foramina and the canal changed during evolution according to the influence that was exerted by the functional interaction between the astragalus, the tibia, and the blood vessels that entered the astragalus.

The various results of such a complex interaction can be described briefly as follows: 1. If the mode of locomotion of a mammal does not

require complete plantar flexion (meaning that the tibia does not completely cover the astragalar trochlea), then the superior astragalar foramen can appear *de novo* and persist or reappear secondarily to allow the traversing of the astragalus by nutrient blood vessels. 2. In mammals that require restrictive plantar flexion (meaning that the tibia completely covers the astragalar trochlea during plantar flexion): (a) the superior astragalar foramen may be closed off and the function of the astragalar canal may be maintained below that foramen for terminal blood vessels branching from the plantar foramen; (b) the astragalus may maintain a non-functional superior astragalar foramen and have the astragalar canal below that foramen for the passage of terminal blood vessels entering from the plantar foramen; (c) the astragalus may completely lack or eliminate both the astragalar foramina and canal. In the last case (c), one foramen or both foramina may be eliminated along with the astragalar canal, and the circulation problem may be solved by capillaries netted over the surface of the bone. 3. The canal and the foramina may be completely retained without any apparent function in the adult animal, as in *Orycteropus*.

The alternatives seem to cover all the possibilities that may result from the interaction of the astragalus, the tibia, and the blood supply of the astragalus.

The evidence for the primitive condition of the astragalus foramina and the astragalar canal in the Mammalia, Theria, Metatheria, or Eutheria is too meager for meaningful conclusions to be drawn. The crucial late Jurassic and Cretaceous fossils are lacking. Most of the Cenozoic record is not very valuable, if one considers the numerous possible changes in the condition of the astragalar foramina in one lineage, particularly when most lineages are never completely documented. Postcranial changes are poorly known, and the available evidence is usually too spotty to be meaningful.

If one restricts oneself to the record of the more primitive mammalian groups, however, some of the evidence may be more profitably explored. Probably the most primitive groups in which the astragalus is known are the Paleocene Leptictidae, the Eocene and early Oligocene Deltatheridia, the Eocene<sup>1</sup> Miacidae, and the Eocene Pantolestidae. These mammals are presumably closer to one another and their common ancestry than some of the later forms with an equally scattered record.

The condition described for *Prodiacodon* is probably fairly representa-

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<sup>1</sup> Mac Intyre (1966, p. 164, fig. 16) illustrated and described a middle Paleocene astragalus (A.M.N.H. No. 12382) very dubiously associated with *Protictis*. This specimen has both the superior and plantar astragalar foramina.

tive of primitive leptictids. These mammals seem to have been scampering and partly scansorial in their mode of locomotion. A functional superior foramen probably would have interfered with plantar flexion, but a plantar astragalar foramen and the canal connected with it were present in *Prodiacodon*. The earliest known deltatheridian astragali are those of the Eocene proviverrine hyaenodontids which had both foramina, although they were rather small compared to the condition seen in the unrelated arctocyonid *Claenodon*. The astragalus of the early Oligocene deltatheridian didymocoid *Didymoconus* (= "*Tshelkaria*" Gromova; J. Mellet, personal communication) reported by Gromova (1952, pp. 44-58) lacks a superior astragalar foramen. I cannot determine from her report whether the plantar foramen and the canal were present or absent.

The evidence bearing on the primitive carnivore astragalus is known with certainty only from the early Eocene. Mac Intyre (1966, pl. 10) figured a specimen of *Didymictis* in which both foramina are clearly present. Matthew and Granger (1915, p. 26, fig. 19) illustrated the astragalus of another species, *Didymictis altidens* (A.M.N.H. No. 14781), which shows the same condition as *Didymictis protenus* figured by Mac Intyre.

The astragalus of the middle Eocene *Pantolestes* (A.M.N.H. No. 12152) has the same condition as is seen in *Prodiacodon* and *Diacodon*.

I am at present inclined to think that both the superior and plantar foramina, as well as the astragalar canal, were primitive and functioned as a clear passage for the nutrient blood vessels of the eutherian astragalus. It is possible, however, that the primitive eutherian condition is reflected in that seen in *Prodiacodon*. Whether the astragalar canal changed as often as the superior astragalar foramen did is less likely. It seems very probable, as stated above, that the superior astragalar foramen appeared, disappeared, reappeared, and persisted in different groups of mammals independently.

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