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EPOICOTHERIID (MAMMALIA, PALAEANODONTA)
FROM THE BIGHORN BASIN, WYOMING**

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SKELETON OF *ALOCODONTULUM ATOPUM*, AN EARLY EOCENE
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KENNETH D. ROSE¹, ROBERT J. EMRY², AND PHILIP D. GINGERICH

Abstract.— A substantially complete skeleton of the early Eocene palaeodont *Alocodontulum atopum* from the Bighorn Basin, Wyoming, is described. It is the oldest and most complete known skeleton referable to the family Epoicotheriidae. *Alocodontulum* was dentally more generalized but postcranially more specialized than the contemporary metacheiromyid *Palaeanodon*. It displays numerous modifications for fossorial habits, which are particularly prevalent in the forelimb skeleton. Certain characters, especially in the manus, foreshadow specializations carried to extreme in subterranean Oligocene epoicotheriids.

INTRODUCTION

Palaeanodonta is an extinct group of early Cenozoic mammals, usually accorded subordinal status, whose members are distinctive in having dentitions with a reduced number of simple teeth and postcranial skeletons with many specializations for digging. Palaeanodonts have often been allied with Edentata (Xenarthra) or Pholidota, but many similar characters shared by these groups may have been acquired independently in response to fossorial habits and a myrmecophagous diet. Existing evidence seems to favor a sister-group relationship between Palaeanodonta and Pholidota, but no special relationship to Edentata (Emry, 1970; Rose and Emry, in press).

Two families of Palaeanodonta are generally recognized: Epoicotheriidae and Metacheiromyidae. Most Epoicotheriidae were more conservative dentally than metacheiromyids but more specialized postcranially, indicating that during their evolution they became progressively more committed to a fossorial and ultimately subterranean existence (e.g., Rose and Emry, 1983). Wasatchian (early Eocene) faunas of the Bighorn Basin include representatives of both families. The epoicotheriid *Alocodontulum* is rather rare, while the metacheiromyid *Palaeanodon* is relatively common. Here we describe an unusually well-preserved skeleton of *Alocodontulum atopum*, which is the most complete known for any member of Epoicotheriidae.

The new skeleton, University of Michigan [UM] 93740, was found by G. F. Gunnell in 1988 at UM locality MP-152 in the Willwood Formation of the McCullough Peaks area,

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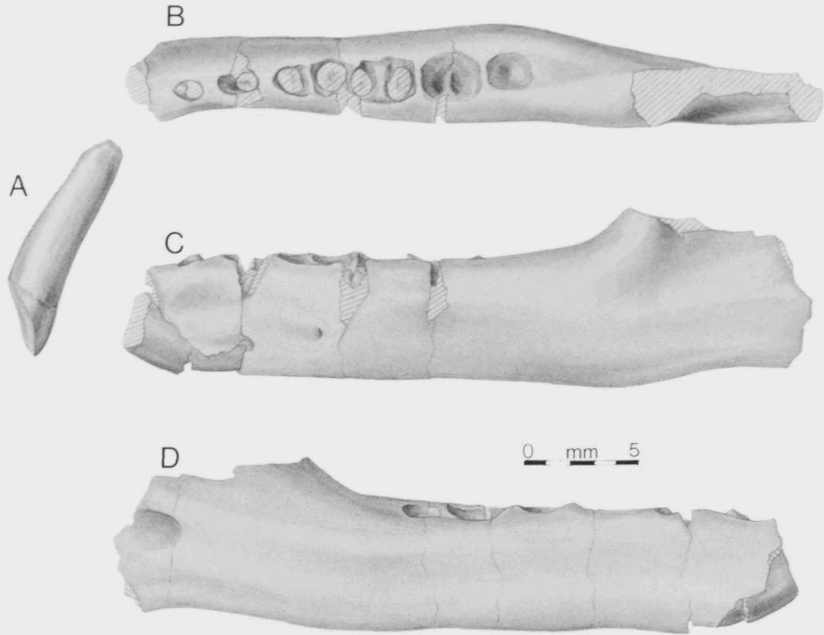


FIG. 1—*Alocodontulum atopum*, UM 93740. A, upper right canine in medial view. B-D, left dentary with roots or alveoli of C, P₂-M₃, in dorsal, lateral, and medial views.

northern Bighorn Basin (NW¼, SE¼, Section 6, T 52 N, R 98 W, Gilmore Hill Quadrangle, Park County, Wyoming). It was found partially articulated, weathering from the side of a low red hill, with numerous jaws and teeth of other small mammals. Some smaller elements of the skeleton were recovered by screen-washing sediment from the site and by repeated examination of the site as it weathered. Eighty catalogued mammalian specimens from MP-152 include *Absarokius metoecus*, *Copecion brachypternus*, and *Vulpavus australis*. The last appearance of *Haplomyilus* in the McCullough Peaks area is about 100 m below MP-152, the first appearance of *Anacodon* is below MP-152, and the first appearance of *Heptodon* is well above MP-152 stratigraphically. All this evidence indicates that UM 93740 comes from the middle part of the *Bunophorus* interval zone of Schankler (1980; =late Graybullian of Granger [1914] and zone Wa-5 of Gingerich [1983, 1991]). *Bunophorus* has not been found at MP-152, but it is present nearby at other localities above and below MP-152.

Alocodontulum atopum was originally based on a single maxillary dentition encased in a hard concretion containing some poorly preserved, presumably associated postcranial remains (Rose et al., 1977, 1978). It is also from the *Bunophorus* interval zone of the Willwood Formation (Yale Peabody Museum locality 348, ~400 m level), but it is not, for the most part, directly comparable to the skeleton described here. Rose (1990) referred a subadult specimen including a few postcranial elements and incomplete dentaries (without teeth) to *A. atopum*, and several undescribed dentary fragments of this species are in the U.S. Geological Survey and University of Michigan collections. We refer UM 93740 to *Alocodontulum atopum* because of its similarity in size to the holotype and other referred specimens (although it is slightly larger than the type), because of its comparable dental structure, and because of its similar age and provenance: *A. atopum* is the only epoicotheriid reported so far from the Willwood Formation.

The postcranial skeleton of UM 93740 is generally similar to that of the Wasatchian metacheiromyid *Palaeonodon ignavus* (Matthew, 1918; Simpson, 1931; Rose, 1990), but it differs in subtle details that more closely resemble the later Wasatchian epoicotheriid *Pentapassalus*. The dentition more closely approximates that of the late Wasatchian epoico-

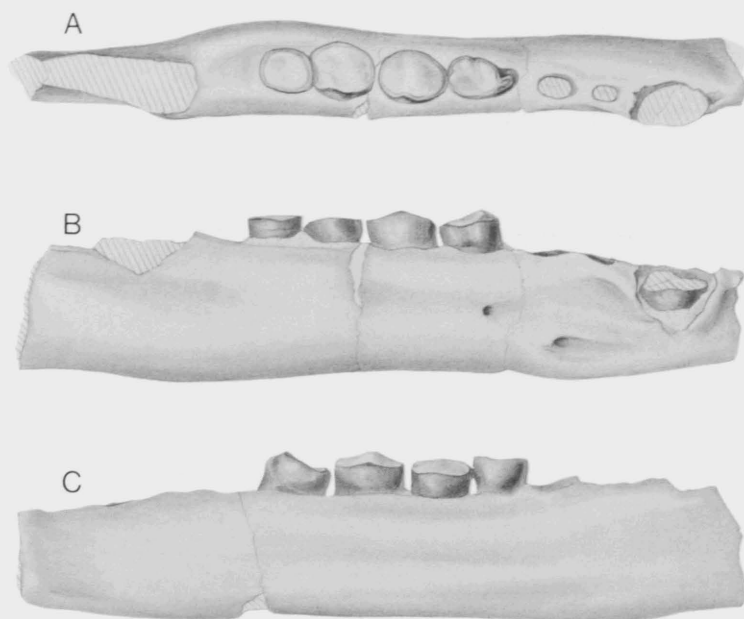


FIG. 2—*Alocodontulum atopum*, UM 93740. A-C, right dentary with P₄-M₃ and roots of the canine and P_{2,3}, in dorsal, lateral, and medial views.

theriid *Tubulodon taylori*. Dental structure suggests that *Alocodontulum*, *Pentapassalus*, and *Tubulodon* are closely allied and possibly synonymous (e.g., Rose et al., 1991). However, we defer consideration of this possibility until completion of a comprehensive study of Eocene palaeonodons currently in progress (Emry and Rose, in prep.).

Comparisons have been made principally with *Palaeonodon ignavus* (described by Matthew, 1918; Rose, 1990), *Metacheiromys dasypus* and *M. marshi* (which includes *M. tatusia*; see Simpson, 1931), and *Pentapassalus pearcei* (Gazin, 1952), as well as with various Pholidota and Xenarthra.

SKULL AND DENTITION

Skull—Several small fragments of the cranium are preserved: a partial left auditory region including petrosal and adhering fragments of squamosal and exoccipital, a fragment of the right petrosal, a fragment of the right exoccipital, right and left occipital condyles, a fragment of supraoccipital from near the junction of nuchal and sagittal crests, and small fragments of maxillary with alveoli or tooth roots. Comparisons are obviously very limited, but insofar as they can be compared, the pieces seem not to differ in any significant way from the corresponding parts of *Pentapassalus pearcei*.

A single upper right canine (Fig. 1A) of typical palaeonodont form (its crown trihedral, with a heavily worn anteromedial wear facet) is the only tooth directly comparable with the holotype of *Alocodontulum atopum*. It corresponds closely in morphology to the upper canine of that specimen and to the upper canines of *Pentapassalus pearcei*; it is the same size as the latter and a little larger than the canine of the type of *A. atopum*. Enamel that remains is very thin and largely restricted to the lateral surface of the crown.

Dentaries—Substantial parts of both dentaries are preserved. The left dentary has roots or alveoli of a large canine and of all the lower cheek teeth, interpreted to be P_{2,4}-M_{1,3} (Fig. 1B-

TABLE 1— Measurements of teeth and dentary of *Alocodontulum atopum*, UM 93740.
All measurements in mm.

		Left	Right
C ¹	Length	---	2.5
	Breadth	---	1.9
P ₄	Length	---	2.8
	Breadth	---	1.8
M ₁	Length	---	3.1
	Breadth	---	2.1
M ₂	Length	---	2.8
	Breadth	---	2.2
M ₃	Length	---	2.4
	Breadth	---	2.0
Dentary	Depth below M ₁ (buccal)	5.5	5.3
	Thickness below M ₁	3.7	3.7

D). The right dentary contains the intact P₄-M₃, as well as roots of the canine and P_{2,3}, and part of an alveolus for a small incisor (Fig. 2). The dentaries are shallow but robust, most similar in structure and size to those of *Tubulodon taylori* and *Pentapassalus pearcei* but not quite as deep as in *Pentapassalus woodi*. The cheek teeth, however, are larger than in these three species (about 15-20% larger in linear dimensions than in *Tubulodon*, and 20-30% larger than in *P. pearcei*). P₄-M₃ are slightly separated from each other as in *Pentapassalus*, not as closely packed as in *Tubulodon*. P₂ and P₃ are set apart by longer diastemata from both the canine and P₄, again as in *Pentapassalus*. Roots indicate that the lower canine was large and slightly compressed mediolaterally, P₂ (the first postcanine) was small and single-rooted, and P₃ was intermediate in size between P₂ and P₄, with one mesiodistally elongated root.

The cheek teeth are heavily worn, as is typical in epoicothores, presenting the appearance of cylinders of dentine surrounded by a thin shell of enamel (compare *Tubulodon taylori*, Rose et al., 1991, fig. 2A). P₄ is two-rooted, although this is only faintly indicated at the base of the crown. It is the only tooth that preserves any remnant of the original unworn crown morphology: traces of what may have been a paraconid or paracristid project mesiad, joining behind with a slightly elevated region probably homologous with the protoconid and, lingually, the metaconid. Posterior to this apparent trigonid is a broader, lower talonid with faint enamel expansions suggesting three talonid cusps. Thus what remains of the crown anatomy appears to indicate a semimolariform tooth similar to that in *Tubulodon* but more molarized. M₁ is clearly two-rooted, whereas the root of M₂ bifurcates deep in its alveolus; M₃ is single-rooted. The crowns are devoid of gross morphology except for low elevations near the middle of the lingual and buccal margins of M₁, giving it a weakly gabled appearance. The buccal side of the molars is slightly higher than the lingual side. In the last two features, these teeth resemble those in the holotype of *Pentapassalus pearcei*. The posterointernal part of the horizontal ramus of the jaw is swollen, forming a prominent medial buttress, a characteristic of most palaeocondonts.

Measurements of the teeth and dentary of UM 93740 are listed in Table 1.

AXIAL SKELETON

Vertebral Column—The vertebral series is evidently complete, except for the tail, although few individual vertebrae have all processes intact (Figs. 3 and 4). Several sections of the series are preserved in articulation. This is the most complete vertebral series reported to date in any palaeodont. Represented are seven cervical, 13 thoracic, and six lumbar vertebrae, as well as the complete sacrum. Fourteen complete caudal centra and parts of four others have been recovered. The tail must have been comparatively long, for even though incomplete distally, the preserved caudals alone would make a tail nearly as long as the entire presacral series. According to Simpson (1931), *Metacheiromys* differed in having 11 thoracic vertebrae, and its tail contained approximately 25 vertebrae. Matthew (1918) had reported 27 postsacral vertebrae associated with a skeleton of *Palaeonodon* (AMNH 15137), but he noted that the specimen included parts of two individuals, rendering the caudal count unreliable.

The centra of cervicals 2-7 are present (Fig. 3A,B), but only fragments of the atlas are preserved. The cervical vertebrae are separate, as in *Palaeonodon* and *Metacheiromys* (the axis is not fused to more distal cervicals as it is in armadillos and some more-derived epicotheres). As in other palaeodonts, the centra are short and dorsoventrally very compressed, with essentially flat dorsal and ventral surfaces. This is reminiscent of the condition in armadillos, but the centra are not so wide relative to other dimensions. C7 is a little longer and more robust than the preceding cervicals. The pronounced dorsal flexure at C7, characteristic of dasypodids and the palaeodont *Dipassalus* (Rose et al., 1991), does not appear to be present. However, without intact neural arches and zygapophyses the absence of the flexure cannot be determined with certainty; if present it was surely less pronounced than in armadillos.

The centra of the first 11 thoracic vertebrae are more or less uniform in size (longer and perhaps slightly narrower than the centra of the cervicals). Those of T12 and T13 are somewhat more robust and have broader, flattened neural spines, which are arrow-shaped in dorsal view with the tip pointing cranial and the "tail" slightly bifurcated (Fig. 3A,C,D). The neural spines of the last three thoracic vertebrae (T11-13) are essentially vertical, not caudally directed as apparently was true of other thoracics. From T3 caudad, the centra are not flat ventrally (as in the cervical region) but are decidedly convex transversely and concave longitudinally, as in *Palaeonodon* (Matthew, 1918). The demifacets on adjoining centra, for articulation with the capitulum of the rib, are poorly defined, again as Matthew observed in *Palaeonodon*.

The transverse processes of at least the first 10 thoracics project laterally from the anterior half of the centrum. Those of T1 are especially strong, wider and longer than on T2 and successive vertebrae, and on each side bear a deeply concave, semicircular, ventrally facing facet for the tubercle of the first rib—suggesting that this rib was robust (see description of ribs below). Thoracics 4-10 have ovoid, slightly rounded (convex) facets on the ventral surface of the transverse processes for the tubercles of the ribs (Fig. 3C,D). The last three thoracic vertebrae have no evident tubercular facets. On T12 and T13 there is a shallow depression on the anterolateral aspect of each centrum (just ventral to the anterolateral remnant of the transverse process)—rather than the demifacets of more anterior thoracics—which presumably accommodated the head of the rib. The transverse processes of T12-13 (and possibly T11, which is damaged), in contrast to those of more anterior thoracics, are differentiated into a prominent metapophysis (=mammillary process) projecting dorsolaterad from the prezygapophysis, a posterolaterally directed anapophysis, and a reduced ridge anterolaterad. Simpson (1931) considered this condition in *Metacheiromys* (especially the prominent metapophyses) to be a special similarity to armadillos; but the metapophyses in *Alocodontulum* are much shorter than in *M. dasypus*, thus resembling certain carnivorans (e.g., *Nasua*) as much as edentates in this region of the vertebral column.

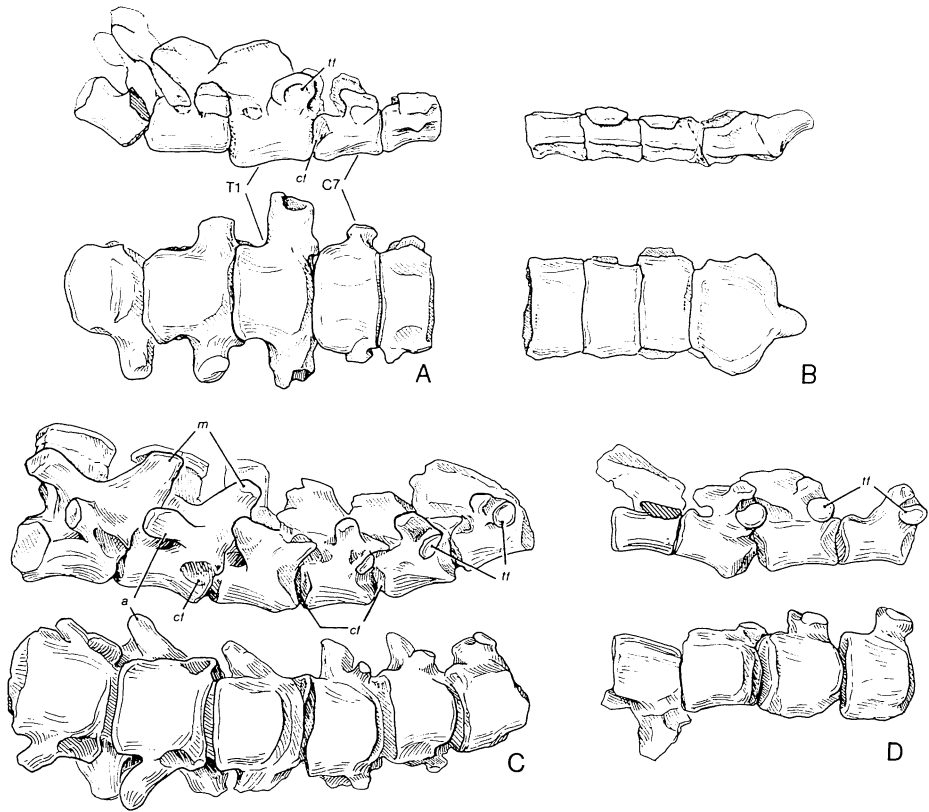


FIG. 3—*Alocodontulum atopum*, UM 93740, cervical and thoracic vertebrae in right lateral and ventral views. A, C6-T3. B, C2-5. C, T8-13. D, T4-7. Abbreviations: C7, seventh cervical vertebra; T1, first thoracic vertebra; *a*, anapophysis; *cf*, capitular facet or demifacets; *m*, metapophysis; *tf*, tubercular facet.

The lumbar vertebrae (Fig. 4A) accentuate some of the characters seen in T12 and T13: their centra increase in size caudally to L5, the metapophyses are craniocaudally more expanded and transversely more widely separated, and the anapophyses are sharper and more spinelike. The anapophyses of the posterior thoracics and lumbar resemble those of various Carnivora rather than the xenarthrous processes of edentates; there is no evidence of accessory (xenarthrous) articulations. Continuous with the anapophysis anteroventrally is a ventrally projecting ridge, sharper and better developed than its counterpart on T12 and T13. The zygapophyses have broad, relatively flat facets, as in *Palaeonodon* (Matthew, 1918). The neural spine of L1 (the only lumbar vertebra in which the spinous process is complete) is similar in shape and height to those of T12 and T13, but conspicuously smaller. The ventral surfaces of the lumbar centra are marked by a pair of vaguely expressed lateral keels (L1-2), fainter lateral keels with a median keel (L3), or a distinct median keel only (L4-6).

The sacrum (Fig. 4A) is complete and definitively consists of three vertebrae, two firmly fused true sacrals and one pseudosacral (=a sacralized caudal) less completely fused to the others. *Palaeonodon* and *Metacheiromys* generally had four sacrals, although at least one specimen of the latter had three (Simpson, 1931). Pholidota have three or four sacral vertebrae (*Manis*; middle Eocene *Eomanis* had four [Storch, 1978], Chadronian *Patriomanis* had three [USNM 299960]). The sacrum of armadillos consists of 7-13 segments. The centrum of the

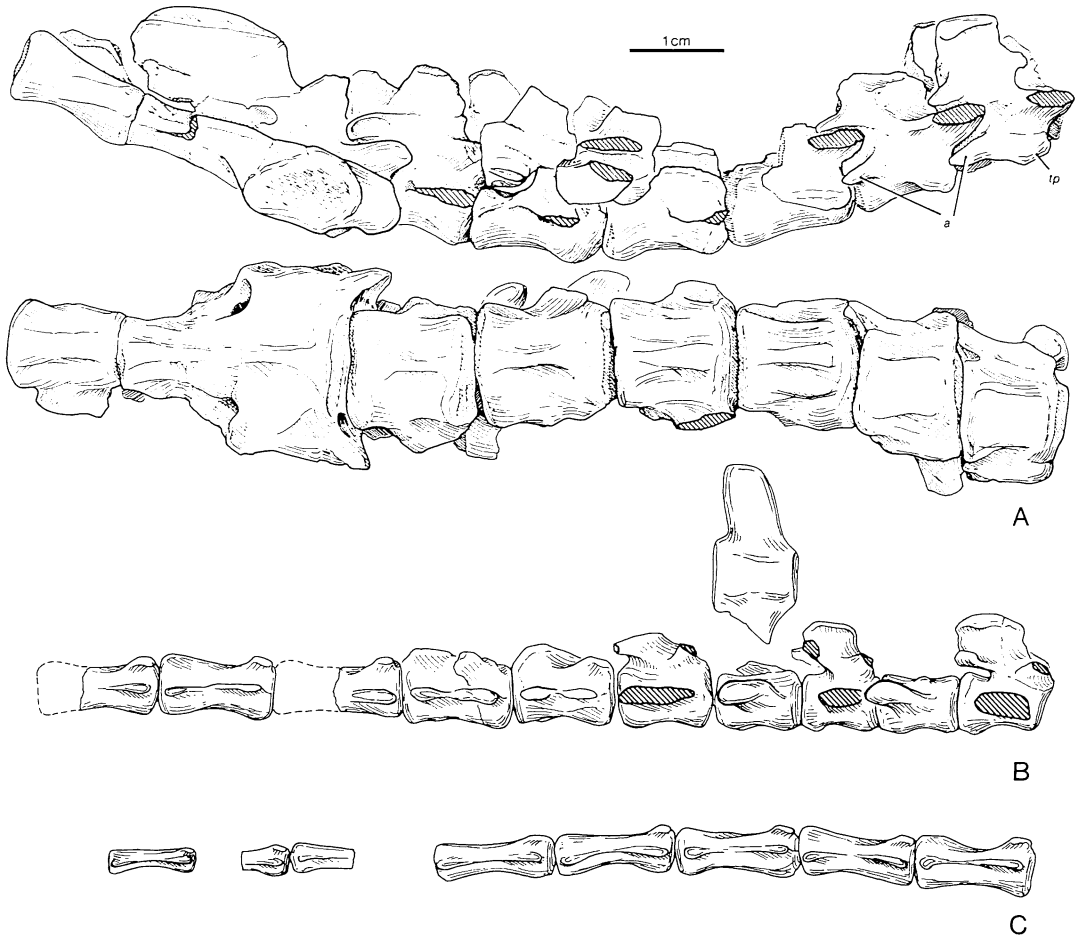


FIG. 4—*Alocodontulum atopum*, UM 93740, lumbar, sacral, and caudal vertebrae. A, L1-6 and sacrum in right lateral and ventral views. B, C, right lateral view of caudal vertebrae; Ca4 also shown in ventral view. Abbreviations: *a*, anapophysis; *tp*, anteroventral part of transverse process.

first sacral in *Alocodontulum* is nearly as robust as those of the distal lumbar, whereas the centrum of S2 is much narrower. The third sacral appears to be slightly more robust than S2. The sacroiliac articulation is more limited than in *Palaeonodon* and *Metacheiromys*, being almost entirely restricted to the first sacral. Though the processes are incomplete caudally, enough is preserved to indicate that the neural spines and zygapophyses of all three sacral vertebrae were fused; the fused spines form a prominent high crest. There is no bony contact between the sacrum and the ischium as occurs in *Xenarthra*.

As noted above, at least 18 caudal vertebrae are represented; they are arranged in probable sequence in Fig. 4B and C. Clearly there are missing vertebrae near the end of the tail, but the first 15 caudals in Fig. 4B-C are probably a complete or nearly complete series. The proximal six or so caudals are robust, with well-developed processes and centra broader than those of the last two sacrals and approaching the caliber of T12 and 13. They have paired keels on the ventral surface, which gradually merge into a single median keel by the eighth caudal. The first (free) caudal is shorter than the third sacral, and the second and third caudals are a little shorter still. The fourth caudal is almost exactly the same length as the first. From Ca4 to Ca12, centrum length progressively increases, and from Ca12 to Ca15, centrum length

TABLE 2— Measurements of vertebral centra of *Alocodontulum atopum*, UM 93740.
All measurements in mm.

		Length	Max. trans. diameter	Dorsoventral diameter
Cervicals	C2 (including dens)	13.3	13.4	3.3*
	C3	5.2	10.2	3.8
	C4	6.2	10.0	3.8
	C5	5.5	10.0	4.1
	C6	6.0	11.2	4.4
	C7	7.4	11.7	4.3
	Thoracics	T1	8.3	10.1
T2		8.7	9.1	---
T3		7.8*	9.1*	4.9
T4		7.8	9.4	4.4
T5		8.2	9.1	4.3
T6		8.2	---	---
T7		7.1*	---	4.6
T8		7.8	9.8	4.5
T9		7.8	10.2	---
T10		7.8	10.5	---
T11		8.3	9.8	---
T12		9.4	10.4	---
T13		9.1	11.6	---
Lumbar	L1	10.6	10.8	6.1
	L2	11.2	11.2	---
	L3	12.7	11.4	---
	L4	12.8	12.1	---
	L5	13.4	12.3	---
	L6	12.6	12.2	---
	Sacrum	S1-3	37.9	20.8
Caudals	Ca1	10.7	9.8	7.1
	Ca2	10.3	9.0	6.9
	Ca3	10.1	8.5	7.1
	Ca4	10.5	9.2	6.8
	Ca5	11.7	8.7	7.2
	Ca6	13.0	8.1	7.7
	Ca7	14.0	8.1	7.3
	Ca8	---	---	---
	Ca9	15.1	7.4	7.2
	Ca10	---	---	---
	Ca11	15.4	6.7	6.6
	Ca12	15.7	6.3	6.3
	Ca13	15.5	5.7	5.7
	Ca14	15.3	5.3	5.4
	Ca15	14.9	4.7	4.9

*Approximate.

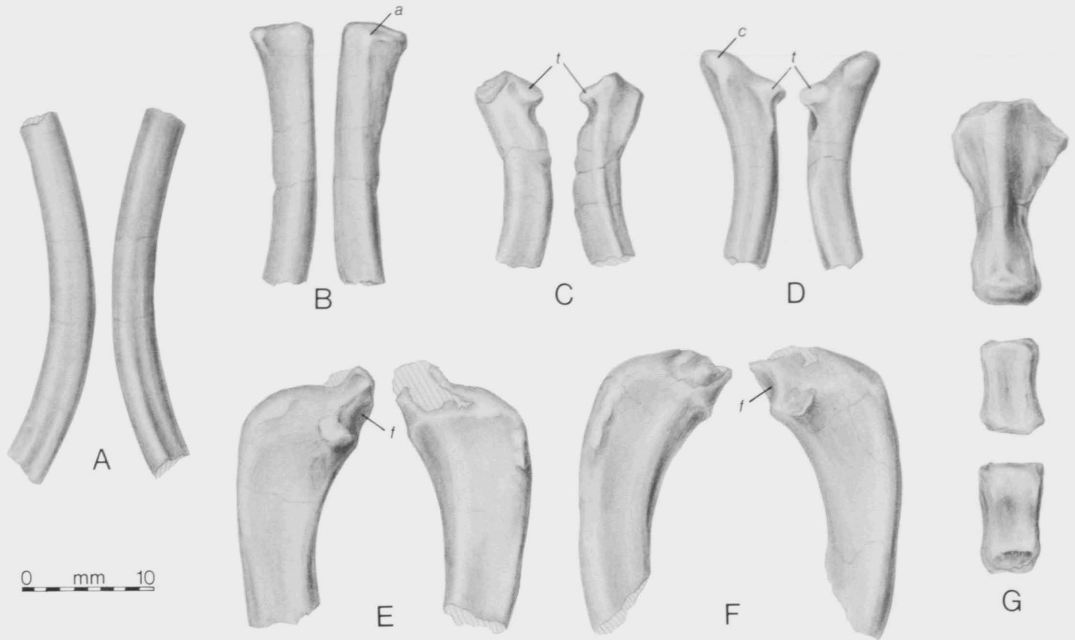


FIG. 5—*Alocodontulum atopum*, UM 93740, ribs and sternal segments. A-D, ribs in anterior and posterior views. E, F, first ribs (?), in anterior and posterior views. G, manubrium sterni (above) and two sternebrae. Abbreviations: *a*, probable articular surface for sternal rib; *c*, capitulum; *f*, apparent articular facet; *t*, articular surface of tubercle.

decreases slightly again. Centrum diameter decreases gradually throughout the series. The spinous process is long, high, and gently caudally inclined on Ca1, lower but still prominent on Ca3; by Ca5, this process is substantially reduced. Caudal to Ca7 all vertebral processes are vestigial.

The proximal caudals at least through Ca5 have massive, broad transverse processes with thick, blunt ends, somewhat reminiscent of those in armadillos and pangolins. Several of these isolated transverse processes were found with the skeleton of *Alocodontulum*, and were subsequently reattached to their centra. They closely resemble a fragment found with *Palaeonodon*, which Rose (1990) tentatively identified as a nonarticulating sternal rib; but their identification in UM 93740 demonstrates that the latter is almost certainly a vertebral process. Postzygapophyses are preserved only on Ca1 and Ca3; they are transversely convex and face ventrolaterad.

Measurements of vertebral centra are listed in Table 2.

Ribs—The several fragmentary ribs preserved with the skeleton are, for the most part, unremarkable (Fig. 5A-D). As Simpson (1931) observed in *Metacheiromys*, the ribs are somewhat craniocaudally compressed, and thicker toward the outer border. The tubercular facets are gently convex craniocaudally but virtually flat mediolaterally.

Two unusual falciform elements (Fig. 5E,F) may be first ribs. They are wider and more robust at one end (presumably the sternal end), which seems to be nearly complete; the narrow (vertebral) end is broken in both. On the concave margin of the wide end is a shallow, apparently articular, facet (for the manubrium?) with a prominent tubercle at its "lower" end. The nature of this facet is uncertain, however, for the joint between the first rib and the manubrium is typically a synchondrosis, not a synovial joint. These curious paired elements (one right, one left) resemble in several details the first ribs of *Manis* (e.g., USNM 198852,

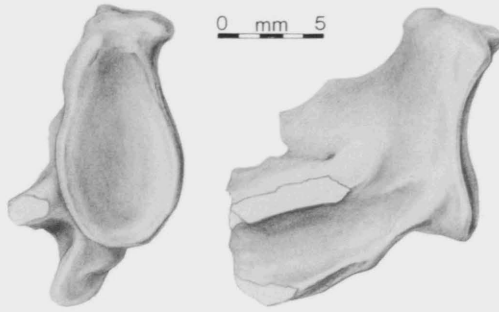


FIG. 6—*Alocodontulum atopum*, UM 93740, glenoid region of right scapula in anterior (left) and lateral views.

294178)—although the latter evidently lack the articular facet—but are quite different from the first ribs of armadillos. Rose (1990) tentatively identified essentially identical bones found with *Palaeanodon* as ossified sternal ribs, and similar elements are known in *Pentapassalus* as well. Ossified sternal ribs are relatively rare among mammals but are characteristic of Xenarthra. Although all these elements do bear similarities to the posterior sternal ribs of armadillos, only one pair has been found with any palaeodont, and they seem to have a closer correspondence with first ribs.

Sternum—Five sternal elements have been identified: the manubrium and four sternebrae (Fig. 5G). The manubrium is narrow but robust caudally (in contrast to the manubrium of armadillos), much wider cranially, and displays a strong ventral keel. It bends ventrad anterior to the rib processes, as in *Metacheiromys* (Simpson, 1931: fig. 14D), though perhaps not so sharply. The sternebrae are block-like and longer than wide, as in *Metacheiromys*. None of these elements are well enough preserved to indicate the manner of articulation of the ribs or costal cartilages.

FORELIMB SKELETON

Scapula—The glenoid portion of both scapulae is preserved (Fig. 6). The glenoid fossa is pyriform, relatively narrower mediolaterally and longer dorsoventrally than in *Metacheiromys* and much closer to these proportions in *Palaeanodon* and *Pentapassalus pearcei*. The coracoid process is prominent and flattened dorsally, and less separated from the glenoid than in metacheiromyids. Although the spine is broken, enough remains to show that it inclines toward the infraspinous fossa. The cranioventral border curves outward, as in *Metacheiromys*, forming a deep, groove-like infraspinous fossa with the spine.

Humerus—Both humeri (Fig. 7A) are substantially complete. They are about 10% longer than the humerus of *Pentapassalus pearcei* and 10% shorter than that of *P. woodi*, and are structurally very similar to the humeri of other early Eocene palaeodonts (*Pentapassalus*, *Palaeanodon*) and the middle Eocene *Metacheiromys*. As in those genera and dasypodid Xenarthra, the humeral head is ellipsoid (longer proximodistally than mediolaterally), and the large greater tubercle projects proximally just beyond the head (right humerus; on the left humerus it is about even with the head), as well as laterally. The lesser tubercle (for insertion of subscapularis) is proximodistally elongate, its distal end projecting mediad from the shaft. The bicipital (intertubercular) groove is narrow and well defined near the head. Descending along the front of the humerus from the greater tubercle is a long, raised pectoral crest which curves laterad toward the capitulum at its distal end and extends a little more than 75% of humeral length. It forms the medial edge of a wide deltopectoral shelf, bounded laterally by

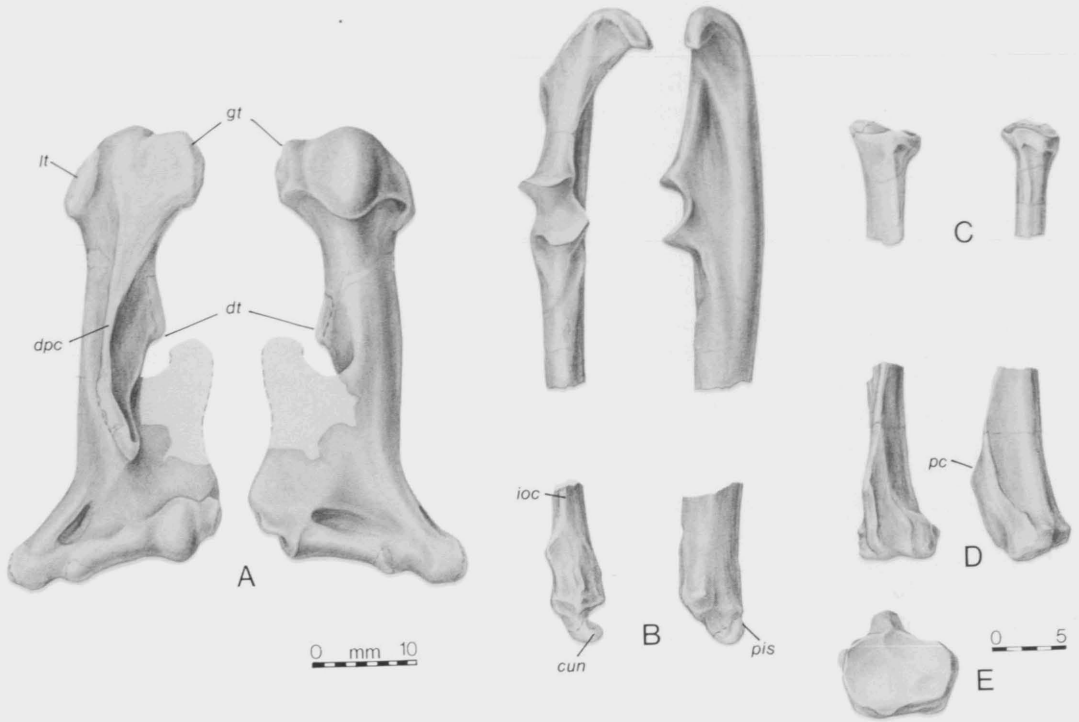


FIG. 7—*Alocodontulum atopum*, UM 93740, forelimb elements. A, left humerus in anterior and posterior views; deltoid tubercle restored from right humerus. B, right ulna in anterior and medial views; short section of midshaft is missing. C, proximal end and D, distal end of right radius, in anterior and medial views; midshaft missing. E, distal articular surface of right radius. Abbreviations: *cun*, cuneiform facet; *dpc*, deltopectoral crest; *dt*, deltoid tubercle; *gt*, greater tubercle; *ioc*, interosseous crest of ulna; *lt*, lesser tubercle; *pc*, pronator crest; *pis*, pisiform facet.

a sharp deltoid crest from which a tubercle projects laterad just proximal to midshaft. The deltoid tubercle is similar in form and slightly more distal than in *Pentapassalus pearcei*, and much more distal than in *Palaeonodon*. On the medial border of the shaft, just opposite the deltoid tubercle, is a faint ridge for attachment of teres major.

The distal end of the humerus closely mirrors that of the other more primitive palaeonodons. It is broad, with a long, medially projecting entepicondyle and, laterally, a broadly expanded supinator crest (=brachial flange or supracondylar ridge). Although the flange is incomplete proximally in both humeri, its junction with the shaft is intact and situated at midshaft. The capitulum is almost hemispherical in anterior perspective, but is constricted to a ridge distally. Both the trochlea and the olecranon fossa are wide and shallow.

Ulna and radius—The right ulna is substantially complete, missing only a small section (probably less than 5 mm) of the distal shaft. Only fragments of the left ulna are preserved, but the distal end including the styloid process is well preserved. Proximal and distal ends of the right radius are present and well preserved; the left radius is essentially complete in length (though broken into three sections), but its articular surfaces are less well preserved. The ulna and the distal radius are robust and anteroposteriorly expanded, recalling the forearm bones of armadillos such as *Dasybus* and *Euphractus* and of the pangolin *Manis*.

The ulnar shaft (Fig. 7B) is mediolaterally compressed, and the olecranon is very large and strongly medially inflected. The semilunar notch is broad and somewhat cylindrical, but also distinctly saddle-shaped (mediolaterally convex). In all these characters, the ulna closely

resembles that of *Metacheiromys dasypus*, and is generally similar to that of the dasypodid *Euphractus*. The shaft differs from those of *M. dasypus* and *Pentapassalus pearcei* in being more deeply excavated both laterally and especially medially near the semilunar notch (perhaps reflecting an especially well-developed flexor digitorum profundus). Its anterodistal border is constricted to form a sharp interosseous crest, as in other palaeonodonts, at the distal end of which is a short lateral projection, set off by what appears to be a shallow (vascular?) groove at its proximal end. Comparable structures are not present in pholidotes or edentates, hence the significance in *Alocodontulum* is uncertain. The styloid process has a narrow, helical articular facet virtually identical to that in *M. dasypus*, which articulated with the cuneiform anteriorly and the pisiform posteriorly. The two facets are essentially confluent.

The radial head (Fig. 7C) is incomplete but appears to be similar to that in *Metacheiromys*, except that the ulnar facet seems to be more nearly flat. The distal end (Fig. 7D) is very similar to that of *Pentapassalus pearcei* and *M. dasypus*, being mediolaterally compressed with a sharp, elevated crest anterolaterally. The most distal part of the crest (about 8 mm long) is higher than more proximally, and is more salient than in *Metacheiromys*, but lacks the sharp tubercle present in *P. pearcei*. Presumably, this crest provided insertion laterally for the supinator muscle (as in *Manis*; Humphry, 1869) and medially for pronator teres, which is a large muscle in armadillos (pronator quadratus is absent in armadillos and *Manis*: Galton, 1870; Windle and Parsons, 1899a). On the medial side of this crest there is a distinct longitudinal ridge which curves posteriad distally. The distal half of the right radius exhibits a short interosseous crest at what was approximately midshaft, just as in *M. dasypus* and stronger than in *P. pearcei*.

The distal articular surface of the radius (Fig. 7E) resembles that of *Palaeonodon* and *Pentapassalus pearcei* and is unlike that of *Metacheiromys* (contra Gazin, 1952) in having weakly separated facets for the lunar and scaphoid, the latter with a shallow excavation on its palmar side.

Carpus—Two carpal elements have been identified, a left cuneiform (=triquetrum) and a left lunar, and several metapodials and phalanges are preserved. While metacarpals and metatarsals can be readily distinguished, assignment of phalanges to manus or pes is less obvious. Some proximal and intermediate phalanges have been assigned on the assumption that the manual phalanges would be relatively stouter and shorter than those of the pes. Ungual phalanges that show relatively greater curvature and mediolateral compression probably represent the manus, whereas broader and flatter unguals are believed to belong to the pes.

The cuneiform (Fig. 8A) closely resembles that of *Metacheiromys dasypus*, differing chiefly in its smaller size, flatter palmar surface, and sharper angle between the two proximal facets (for the ulna dorsolaterally and the pisiform toward the palmar side).

The lunar (Fig. 8B) is also very similar to its counterparts in *M. dasypus* (see Simpson, 1931) and *Pentapassalus pearcei* (Gazin, 1952). It is much greater in dorsoventral depth than in mediolateral width (depth:width = 1.61). The radial facet is strongly convex, describing a dorsoventral arc of a little more than 90° along its medial (scaphoid) border, such that the facet extends dorsally to the distal edge of the bone. In this it resembles both *P. pearcei* and *M. dasypus*; the apparent difference between the latter two species in dorsal extent of the radial facet reported by Gazin (1952, p. 42) results from breakage in *M. dasypus*. It also resembles the lunar of these taxa in having a prominent, gently rounded palmar process, which may have contacted a sesamoid in the tendon of flexor digitorum profundus (as in *Manis*, dasypodids, and the Chadronian palaeonodont *Xenocranium*: Humphry, 1869; Windle and Parsons, 1899a; Rose and Emry, 1983), thereby increasing the leverage of the digital flexors.

Manus—The left second and third metacarpals (Fig. 8C-E) are complete and very similar to those of *Pentapassalus pearcei* and *Metacheiromys dasypus*. They are short (though Mc III is about 40% longer than Mc II), very robust, and slightly arched, with small dorsal rugosities marking attachment of the tendons of extensor carpi radialis.

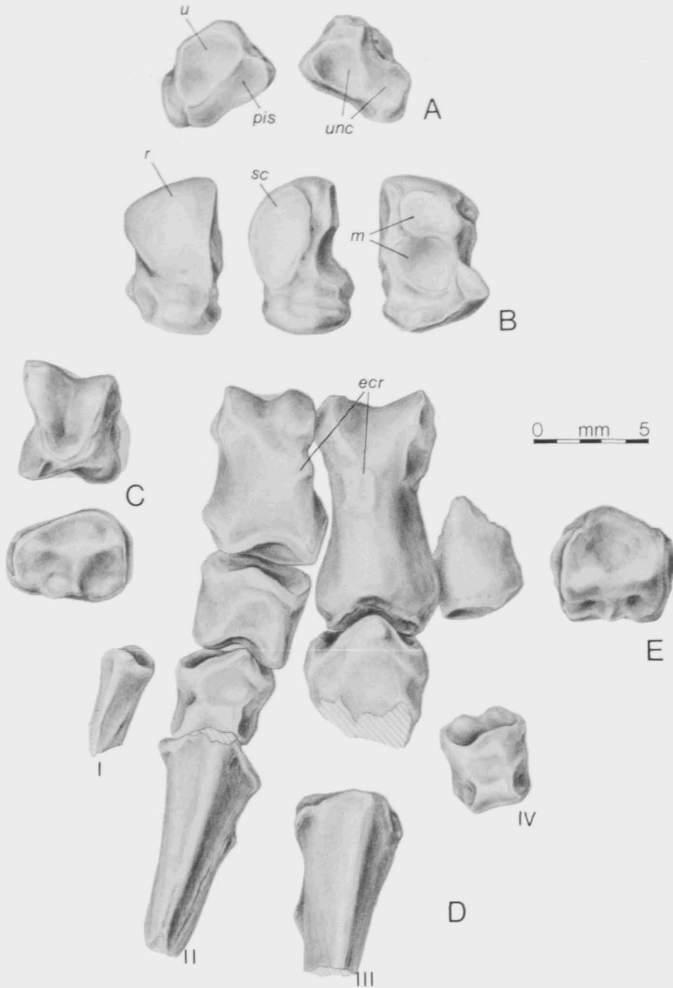


FIG. 8—*Alocodontulum atopum*, UM 93740, carpal elements and manus. A, left cuneiform in proximal and distal views. B, left lunar in proximal, medial, and distal views (left to right). C, left metacarpal II, in proximal view (above) and distal view (below). D, reconstructed left manus. E, left metacarpal III, distal view. Dorsal is at top in all views except D. Abbreviations: *ecr*, insertion sites of extensor carpi radialis; *m*, facets for magnum; *pis*, facet for pisiform; *r*, facet for radius; *sc*, facet for scaphoid; *u*, facet for ulnar styloid; *unc*, facet for unciform.

The proximal end of both metacarpals (Fig. 8C) is more or less quadrate, notched on the dorsal border, and thick and somewhat grooved in the dorsopalmar plane. That of Mc III is wider dorsally than ventrally (and wider than proximal Mc II) and has irregular processes at the four corners. The dorsal part of the proximal articular surface of Mc II (much better preserved than that of Mc III) is reminiscent of an astragalar trochlea, with a deep dorsoventral groove separating a pair of condyles, the lateral one longer than the medial one—a configuration that presumably would have limited movement at this joint to flexion-extension. At the palmar end of the groove is a broad concavity, bounded ventrally by an irregular transverse ridge that joins a pointed lateral tubercle to a bulbous medial tubercle.

The distal articular surfaces are also unusually specialized. On Mc II (Fig. 8C) the dorsoventral curvature of the surface is so tight as to present the appearance of a transverse

ridge that divides the facet into a smaller, nearly flat surface facing distad and somewhat dorsad, and a larger palmar-facing facet consisting of a pair of depressions separated at the base by a short median spine, the remnant of a keel. This structure is reminiscent of, but seemingly even more specialized than, that in the armadillo *Dasybus*. On Mc III, the distal surface is transversely cylindrical, with a smaller pair of ventral depressions separated by a larger spine (Fig. 8E). The dorsal margin on Mc III is notched and confluent with a fossa to accommodate an extensor projection from the proximal phalanx.

The distal end of left Mc IV is also preserved. Its phalangeal articulation approximates a mirror image of that of Mc II, but it is smaller, the dorsal part is more cylindrical, and the palmar spine (keel) is larger.

Another, somewhat damaged, manual metacarpal associated with this skeleton appears to represent the left Mc III (a little shorter than the one just described) of a second individual.

Phalanges probably from the manus (applying criteria mentioned above) include proximal phalanges of the second and third digits, intermediate phalanges of digits II and IV, and terminal phalanges of the central and lateral digits (Fig. 8D). To facilitate description, we shall refer to them by digit, then phalangeal position: e.g., II-1 is the proximal phalanx of digit II. The proximal phalanges are short and robust, wider than long. The proximal articular surface of phalanx II-1 is transversely concave but subtly separated into a small medial depression and much larger lateral depression, to accommodate corresponding irregularities on the distal surface of Mc II. The palmar half of this articulation is essentially a pair of convex condyles, separated by a broad ventral notch. Dorsally a process whose contour matches that of the dorsal margin of the distal articulation of Mc II projects back toward the metacarpal. The distal articulation consists of a pair of elongate condyles, about half the length of the phalanx, which face distad and mostly palmad; they are separated by a dorsoventral groove, at the palmar end of which is a weakly-developed tubercle, as in *Metacheiromys* (Simpson, 1931). Because none of the articular surface is exposed dorsally, the distal end of these phalanges appears incomplete in dorsal view. Phalanx III-1 is damaged distally but is apparently almost complete, despite its peculiar wedge shape in lateral profile. Its proximal articular surface is concave; on its palmar margin is a pair of rounded tubercles separated by a notch for the vestigial keel of Mc III, and dorsally there is a pronounced extensor process (much bigger than in II-1) that projects proximally and fits into a depression on Mc III. The latter structure seems to have prevented hyperextension of the proximal phalanx. The distal articulation appears to have been similar to that of II-1 and other proximal phalanges.

The intermediate phalanges, except for being short and stout, are morphologically more like typical phalanges. The proximal articular surface consists of a pair of shallow depressions for the proximal phalanx, and a dorsal (extensor) process a little smaller than that of the proximal phalanges. The distal end has an extensive articular surface which is cylindrical (but higher at the margins and depressed slightly in the middle) and curves through an arc of more than 180°, extending from the dorsal to the palmar surface.

The terminal phalanges of the central digits are large and somewhat curved, with prominent, elongate flexor tubercles. (A much smaller possible lateral ungual has also been identified.) Smaller extensor processes were also present but are broken off most of the unguals. Though laterally compressed, they are transversely wider on the palmar aspect than on the dorsal margin, which comes to a sharp crest. A narrow fissure (much less conspicuous than the deep fissure in manids, including *Patriomanis*) is present distally on the most complete ungual, believed to pertain to digit II, as are vascular grooves near the ventral margin of the shaft on all terminal phalanges.

Measurements of forelimb elements of UM 93740 are listed in Table 3.

HIND LIMB SKELETON

Pelvis—The bony pelvis (Fig. 9) is substantially intact: the ilia and ischia of both sides are nearly complete, but both pubes are missing except for a short part of the acetabular rami, and a fragment possibly from near the right pubic symphysis. The pelvis corresponds in almost all details to those of *Palaeanodon*, *Metacheiromys*, and *Pentapassalus*. The ilium is long and narrow, directed outward and only slightly expanded at its proximal end. Except at its most proximal extent, it is triangular in cross-section, with medial, dorsal, and ventrolateral surfaces. The latter two meet at an angle a little less than 90° along the distinct but rounded lateral crest. Just anterior to the acetabulum is a rough, somewhat swollen eminence for origin of the rectus femoris. Inferior to this on the ventral margin is a larger tubercle, the iliopubic eminence. The ischial tuberosity is prominent and everted. In contrast with metacheiromyids (Matthew, 1918; Simpson, 1931), the ischial ramus is not in direct line with the ilium but rather angles about 25° dorsad relative to the iliac blade, as in *Pentapassalus pearcei*.

Femur—Both femora are nearly complete; the left femur is missing a small part of the midshaft including the third trochanter (Fig. 10A). Like other parts of the skeleton, the femur is relatively short and robust. It is indistinguishable from that of *Pentapassalus pearcei* except for being about 23% longer (and proportionately stouter).

The greater trochanter projects proximally slightly less than the head, as in manids (but contrasting sharply with the high and prominent greater trochanter of armadillos). Similarly, the lesser trochanter is expressed to the same degree as in manids, much less than in armadillos. The trochanteric fossa is moderately deep, whereas the intertrochanteric line can barely be detected. A moderately developed third trochanter is situated about 40% of total femoral length distal to the head, similar to the position in *Pentapassalus* but relatively more distal than in *Xenocranium*. The femoral shaft is about 50% broader in mediolateral diameter than in anteroposterior diameter (depth), and the distal end is also much broader than deep. The patellar groove, however, is relatively narrow compared to the breadth of the distal end, and is clearly grooved rather than flat, but this is not unlike the situation in other palaeanodonts (except Oligocene *Xenocranium*: Rose and Emry, 1983). Similarly, as in *Metacheiromys*, *Pentapassalus*, and *Xenocranium* (see Simpson, 1931; Gazin, 1952; Rose and Emry, 1983), the medial femoral condyle projects farther distad and posteriad than the lateral condyle.

Patella—This element is almost square, about 10% longer proximodistally than wide, and otherwise unremarkable.

Tibia—Both tibiae are essentially complete, except that the right one is missing most of the lateral condyle. The tibia (Fig. 10B,C) closely resembles those of *Pentapassalus* (so far as they can be compared), *Palaeanodon*, and *Metacheiromys*. It is conspicuously shorter than the femur (crural index = .86). The shaft is bowed in both coronal and sagittal planes, resulting in slightly concave lateral and posterior borders (but less so than in the type specimen of *Pentapassalus pearcei*, Gazin, 1952: fig. 4B, which exaggerates the actual condition). The lateral half of the proximal end projects laterad to such an extent that the shaft appears to be situated asymmetrically below the medial condyle. Proximally the shaft is roughly triangular and about 50% greater in anteroposterior than in mediolateral dimension. The medial surface is convex and broad, especially proximally, the lateral surface (housing tibialis anterior) is concave, and the narrower posterior surface is nearly flat or slightly concave. Near the distal end the shaft is almost round, then abruptly expands to become transversely broad.

The tibial condyles (plateaus) are of markedly unequal height and contour, the medial one lower and mediolaterally concave (its lateral margin elevated to a sharp intercondylar spine) and the lateral one higher and slightly convex (more so posteromedially). A faint depression at the posterolateral border differentiates the articular surface of the lateral condyle from a posteriorly-facing convex articular facet (though the two facets are continuous), which presumably contacted a sesamoid in the popliteus tendon (variously called a fabella, e.g., Evans

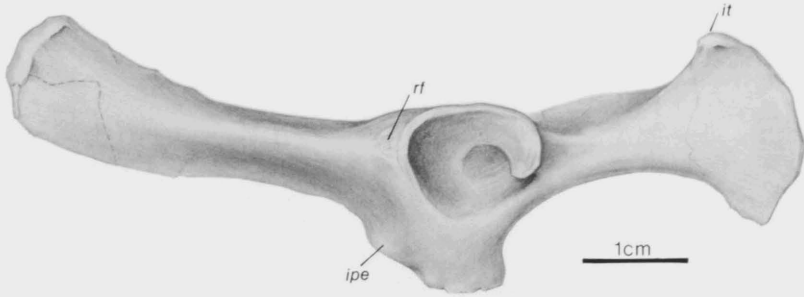


FIG. 9—*Alocodontulum atopum*, UM 93740, left bony pelvis; part of ilium restored from right side. Abbreviations: *ipe*, iliopubic eminence; *it*, ischial tuberosity; *rf*, origin site of rectus femoris.

and Christensen, 1979, or a *cyamelle*, Lessertisseur and Saban, 1967, to distinguish it from the sesamoids of the gastrocnemius). This sesamoid is present in manids, myrmecophagids, bradypodids (but not dasypodids), and evidently metacheiromyids (Windle and Parsons, 1899b; Emry, 1970), as well as many insectivorans, bats, primates, carnivorans, and rodents (Lessertisseur and Saban, 1967). The inferior surface of the projection bearing the popliteal facet has an elliptical facet for the head of the fibula.

The tibial tuberosity (for the patellar ligament) is marked by a low transverse ridge just distal to the proximal articulation. The cnemial crest originates as a line arching medially from the lateral side of the tibial tuberosity to the anterior aspect of the shaft, and descends beyond midshaft, where it terminates as a low but distinct, elongate tuberosity situated about 60% of total tibial length from the proximal articular surface. This presumably provided relatively distal insertions for semitendinosus and perhaps gracilis and sartorius (flexors of the knee).

On the posterior aspect, a sharp crest forms the medial border of the proximal third of the shaft, from just below the medial condyle. This crest may be a reflection of the relative size and importance of the popliteus muscle, which presumably attached here and (as noted above) had a sesamoid in its tendon, and which is known to be large in manids and most xenarthrans (Windle and Parsons, 1899b). The medial collateral ligament attaches at the distal end of a similar crest in dasypodids. A second crest (soleal or popliteal line) runs parallel to this crest about 2 mm lateral to it, presumably marking the medial origin of flexor digitorum longus and/or tibialis posterior.

The distal tibia is transversely expanded and bears a pair of depressions (separated by an anteroposterior ridge) on its articular surface for the astragalus. A crescentic fibular facet (indicating a synovial joint), facing laterally, is situated just proximal to the lateral part of the astragalus (Fig. 10B). Above the fibular facet is a rough triangular depression, which accommodated a small fibular tubercle in what was evidently a syndesmotomic (not synovial) joint. The medial malleolus is of modest size; on its posterior aspect is a distinct sulcus for the tendon of tibialis posterior.

Fibula—Distal ends of both fibulae are present, that of the left side being substantially better preserved and furnishing the following details (Fig. 10B). Facing distomedially is a semicircular facet (for the lateral surface of the astragalus), which adjoins the trochlear facet of the tibia. Immediately proximal to it is a crescentic facet matching that of the tibia. Proceeding more proximally, there is a short (7 mm) interosseous crest (opposing that of the tibia) anterior to a tubercle that fits into a tibial depression (alluded to above); above this point the shaft rapidly constricts to become more than twice as deep anteroposteriorly as in transverse dimension. A small process with a poorly defined peroneal groove projects laterad from the lateral malleolus.

To judge from the known articular surfaces (proximal on the tibia, distal on both tibia and fibula), the proximal tibiofibular joint was synovial, whereas the distal joint was synovial and

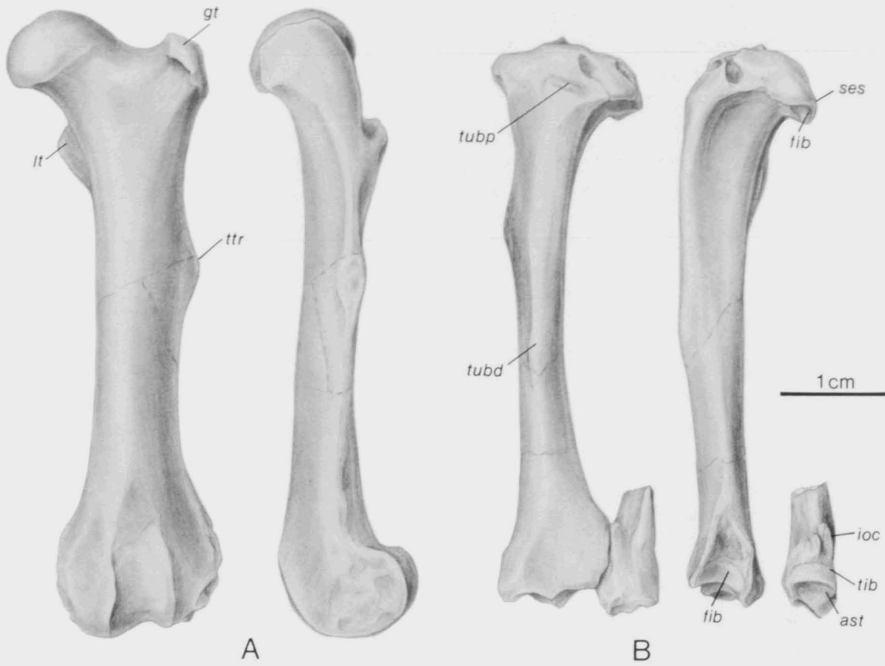


FIG. 10—*Alcocodontulum atopum*, UM 93740, hind limb elements. A, left femur in anterior and lateral views (partly restored from right femur). B, left tibia in anterior and lateral views; distal fibula is shown in anterior and medial views. Abbreviations: *ast*, astragalar facet; *fib*, fibular facet; *gt*, greater trochanter; *ioc*, interosseous crest; *lt*, lesser trochanter; *ses*, facet for popliteal sesamoid; *tib*, tibial facet; *ttr*, third trochanter; *tubd*, distal tibial tuberosity; *tubp*, proximal tibial tuberosity.

probably syndesmotic just proximal to the synovial articulation. The fibula of UM 93740 was therefore of the intermediate type of Barnett and Napier (1953), which according to these authors occurs in *Canis*, *Vulpes*, *Sus*, and *Tapirus* (cursorial taxa), and such diggers as *Meles* (Old World badger), and *Myrmecophaga*. It contrasts with the condition in dasypodids and the derived epiocotheriids *Xenocranium* (Rose and Emry, 1983) and *Dipassalus* (Rose et al., 1991) in which the tibia and fibula are synostosed at both ends.

Tarsus—Each of the seven tarsal elements is preserved on one side or the other: left astragalus (broken posteroventrally), calcaneus, ecto- and mesocuneiform; right astragalus head, distal calcaneus, cuboid, and navicular; and a ?left entocuneiform (Figs. 11-13).

The astragalus (Fig. 11A) is similar to that of *Palaeonodon* except that the body is markedly shallower dorsoventrally (as in *Dipassalus*), and the neck is relatively very short; in these respects it is more like that of *Pentapassalus woodi*. The calcaneal facets resemble those of *Palaeonodon*. This astragalus differs from those of other palaeonodonts in having a more gently rounded medial trochlear ridge and a small excavation on the dorsal side of the neck (which accommodated a small tibial process during dorsiflexion).

The calcaneus (Fig. 11D) is relatively short, with its astragalar facets distally situated. The orientation of articular facets corresponds to that in *Palaeonodon*, but in UM 93740 the posterior astragalar facet is shorter and appears to be arranged more transversely. A prominent peroneal tubercle (nearly as big as the sustentaculum tali) is intact on the right calcaneus. Both the peroneal tubercle and the sustentaculum are located just proximal to the cuboid facet. The latter is markedly narrower transversely than dorsoventrally, and is bounded ventrally by a plantar tubercle of moderate size.

TABLE 3— Measurements of limb elements of *Alocodontulum atopum*, UM 93740. Lengths are measured from proximal to distal articular surface. All measurements in mm.

		Left	Right
Scapula	Glenoid fossa, length	---	9.5
	Glenoid fossa, width	---	6.3
Humerus	Length (head to trochlea)	41.4	41.0
	Length of deltopectoral crest ¹	31.2	---
	Head, length	11.7	11.6
	Head, width	7.9	7.9
	Distal (epicondylar) breadth	---	21.8
Ulna	Length of olecranon (to mid notch)	---	20.3
Radius	Length	31.3*	---
Lunar	Maximum dorsoventral dimension	6.8	---
	Maximum proximodistal dimension	3.9	---
	Maximum mediolateral dimension	4.4	---
Mc II	Length	7.2*	---
	Breadth (proximal, midshaft, distal)	4.2, 4.4, 5.3	---
Mc III	Length	9.9	---
	Breadth (proximal, midshaft, distal)	5.5, 3.9, 5.5	---
Phalanx II-1	Length	3.7	---
	Breadth of proximal end	5.2	---
Phalanx III-1	Length	4.5*	---
	Breadth of proximal end	5.4	---
Pelvis	Ilium length	42.0*	42.0*
	Ischium length	29.0*	29.0*
Femur	Length (head to condyles)	60.5	60.2
	Distal end, transverse breadth	15.7	16.8
	Distal end, anteroposterior depth	12.4*	12.7
Patella	Length	6.6	---
	Breadth	6.1	---
Tibia	Length	52.1	51.8
	Proximal transverse breadth	15.0	---
	Distal transverse breadth	9.8	10.1
Calcaneus	Length	17.4	---
Astragalus	Length	10.0*	---
	Breadth of trochlea	7.8	---
Cuboid	Maximum dorsoventral dimension	---	5.5
	Maximum proximodistal dimension	---	5.9
	Maximum mediolateral dimension	---	4.1
Mt I	Length	---	6.5
Mt II	Length	13.9	14.1
Mt V	Length	---	9.8
Phalanx II-1	Length ²	4.7	---
	Breadth of proximal end	5.7	---
Phalanx II-2	Length	5.3	---
	Breadth of proximal end	4.8	---
Phalanx III-1	Length	4.5	---
	Breadth of proximal end	5.6	---
Phalanx III-2	Length	4.9	---
	Breadth of proximal end	4.6	---

*Approximate.

¹From greater tuberosity to distal end.²Phalangeal lengths measured from proximal articulation to intercondylar groove.

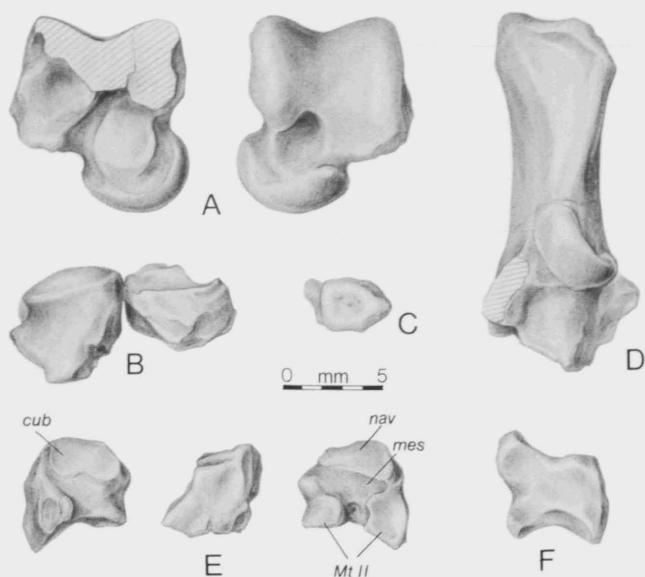


FIG. 11—*Alocodontulum atopum*, UM 93740, tarsal elements. A, left astragalus in ventral and dorsal views. B, right cuboid and navicular in dorsal view. C, left mesocuneiform in dorsal view. D, left calcaneus in dorsal view. E, left ectocuneiform in lateral, dorsal, and medial views (left to right). F, left entocuneiform in lateral view. Proximal is at top in all views. Abbreviations: *cub*, facet for cuboid; *mes*, facet for mesocuneiform; *Mt II*, facets for metatarsal II; *nav*, facet for navicular.

The proximal surface of the navicular is deeply excavated to receive the astragalus head, whereas the distal surface bears three distinct facets, for the cuneiforms. The facets for the ecto- and mesocuneiform are deeper dorsoventrally than wide, the former being somewhat sellar (slightly concave dorsoventrally and convex transversely), the latter convex in both dimensions but more so transversely. Distomedially is a smaller facet (broken medially), more strongly convex dorsoventrally and facing mediolateral, for the entocuneiform. The cuboid facet is flat, not convex as in *Metacheiromys* (Simpson, 1931). The distinctive ventromedial hooklike process mentioned by Matthew and Simpson (in metacheiromyids) is broken off.

The navicular resembles that of metacheiromyids in having a large plantar process with a smooth, apparently articular surface that may have contacted a sesamoid bone (Matthew, 1918; Simpson, 1931), analogous to the palmar sesamoid in palaeonodons and some other fossorial mammals. A much smaller plantar process is present on the cuboid. Similar plantar tubercles occur in some dasypodids, where they contact a plantar sesamoid within either the annular tarsal ligament (Simpson, 1931; Lessertisseur and Saban, 1967) or the tendon of the flexor digitorum (Macalister, 1873). In *Manis*, however, these processes are covered by ligaments and do not articulate with a sesamoid (Humphrey, 1869).

The cuboid (Fig. 11B) is similar overall to that of *Metacheiromys*. Its proximal (calcaneal) facet is strongly oblique, quadrate, deeper laterally than medially, and convex in both dimensions. The distal facet (for Mt IV and V) is more transversely oriented. Medially the cuboid has a large, weakly convex, more or less quadrate facet for the navicular and ectocuneiform. A deep vertical groove separates this facet from the distal articular surface. On the distoplantar aspect, a deep transverse groove accommodated the tendon of peroneus longus. Just proximal to the peroneal groove is the small, rounded plantar process mentioned above, which probably contacted a sesamoid.

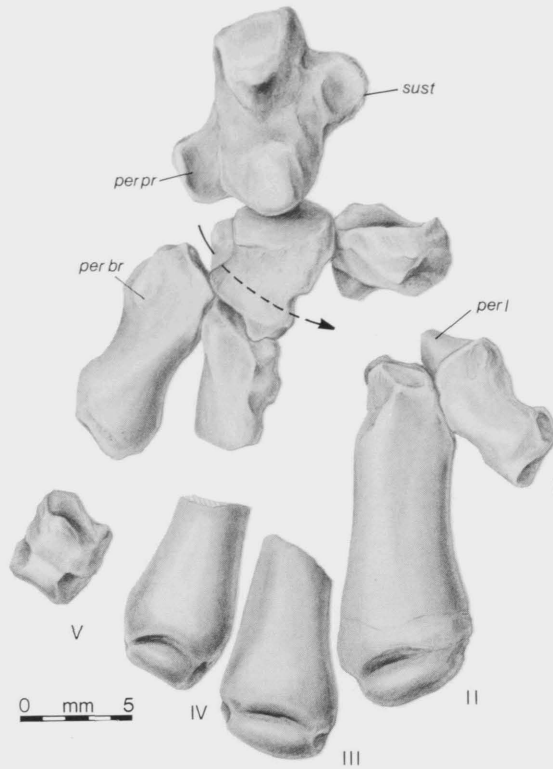


FIG. 12—*Alocodontulum atopum*, UM 93740, reconstructed partial right foot, showing calcaneus (partial), cuboid, navicular, metapodials, and one phalanx; *per br*, tubercle for insertion of peroneus brevis; *per l*, process for insertion of peroneus longus (attachment on plantar surface); *per pr*, peroneal process; *sust*, sustentaculum tali. Arrow indicates pathway of peroneus longus in sulcus on plantar surface of cuboid.

The ectocuneiform (Fig. 11E), in dorsal perspective, is somewhat trapezoidal, broader distally than proximally, and slightly longer than broad. However, its greatest dimension is in the dorsoventral plane, especially distally. As in *Metacheiromys* (Simpson, 1931), the proximal and distal articulations are obliquely oriented and subparallel, more proximal on the lateral side. The ectocuneiform articulates distally with Mt III, proximally with the navicular, and laterally with the cuboid. Most of the medial surface is taken up by extensive dorsal and ventral facets for articulation with Mt II; proximally there is a narrow facet for the mesocuneiform. The mesocuneiform (Fig. 11C) is quadrangular dorsally, wider than long (proximodistally). Like the ectocuneiform, it is much deeper dorsoventrally than it is wide or long. The proximal and dorsal surfaces are roughly triangular; the proximal facet (for the navicular) is a shallow depression, whereas the distal facet (for Mt II) is concave in dorsoplantar dimension. The entocuneiform (Fig. 11F) is a deep, mediolaterally compressed element with markedly concave proximal and distal articular surfaces; its lateral surface is poorly preserved and articular facets cannot be discerned.

Pes—All or part of each metatarsal is represented on one side or the other: right Mts I?, II, III (distal half), IV (proximal and distal ends), and V, and left Mts II, III (proximal and distal ends), and V (complete save for the distal articulation). These are illustrated in Figures 12 and 13. Aside from being relatively short, the metatarsals are less specialized than the metacarpals. The first and fifth metatarsals are markedly smaller than the others, which increase in robustness in the sequence Mt IV, Mt III, Mt II. Although relative lengths cannot

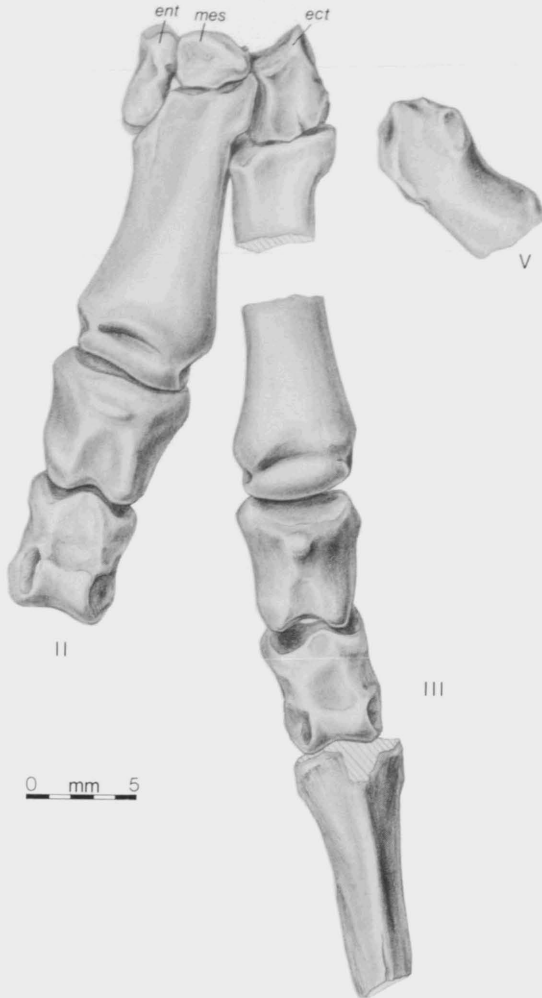


FIG. 13—*Alocodontulum atopum*, UM 93740, reconstructed partial left foot, showing cuneiforms and parts of digits II, III, and V. Abbreviations: *ect*, ectocuneiform; *ent*, entocuneiform; *mes*, mesocuneiform.

be determined for all metatarsals in UM 93740, Mt I was clearly the shortest and Mt V next shortest. In *Metacheiromys* Mts III and IV are of approximately equal length and are slightly longer than Mt II; it is quite likely that this pertained to *Alocodontulum* as well.

The metatarsals have less modified proximal ends than the metacarpals. As Simpson (1931) observed, the tarsal arrangement is essentially serial: Mt I articulates with the entocuneiform, Mt II with the mesocuneiform proximally, the ectocuneiform laterally, and the entocuneiform medially (Fig. 13), Mt III with the ectocuneiform, and Mts IV and V with the cuboid. Proximally, on lateral and/or medial aspects, the metatarsals also have facets for articulation with adjacent metatarsals (e.g., a crescent-shaped facet on matching surfaces of Mts IV and V; others are less clearly discerned). A conspicuous proximal projection on the plantar surface of Mt I marks the insertion of peroneus longus, while a rugosity proximolaterally on Mt V was presumably the site of insertion of peroneus brevis.

The distal articulation of all the metatarsals except Mt V is more or less cylindrical; on Mt V it is flat to slightly concave more dorsally. Mts I and V, as would be expected, are more

TABLE 4— Body size determination for Eocene epicotheriid *Alocodontulum atopum* based on measurements of UM 93740. Predictions computed using program in Gingerich (1990).

<i>Alocodontulum atopum</i>	Measurement (mm)	Predicted body mass (g)	95% Prediction limits	
			Min (g)	Max (g)
Humerus length	41.2	578	171	1,959
Ulna length	55.4*	776	245	2,453
Metacarpal length	9.9	251	40	1,589
Femur length	60.3	943	258	3,447
Tibia length	51.9	359	97	1,329
Metatarsal length	14.1	145	22	967
Humerus diameter	6.8	2,340	1,291	4,241
Ulna diameter	5.9	—	—	—
Metacarpal diameter	4.3	8,276	3,396	20,172
Femur diameter	5.9	1,502	790	2,856
Tibia diameter	6.3	2,175	854	5,535
Metatarsal diameter	2.9	1,486	398	5,553
N, geom. mean, max., min.	11	963	3,396	967
Multiple regression	All species: (Artiodactyla removed):	11 L&D— 2,217 (2,108)	6 L— 631 (555)	

*Estimated

asymmetrical than the others, with sharply oblique distal ends. On both of these metatarsals the phalangeal articulation faces distad and plantad, with no dorsal extension. Viewed end-on, this articulation in Mt I is trapezoidal, much thicker laterally than medially. The phalangeal articulations of Mts II-IV extend dorsally but are lower than, not even with, the phalangeal shaft, thus forming a transverse pit that effectively limited phalangeal extension. Like Mts I and V, Mt II has a strongly oblique distal end. The median keel on the distal articular surface of all five metatarsals is short, spinelike, and fully ventral.

A few phalanges (Fig. 13) are tentatively identified as belonging to the pes because they are relatively longer than those of the manus (although still very short and robust). They resemble those of the manus in having distoplantar-facing distal articulations on the proximal phalanges but more dorsally extensive distal facets on the intermediate phalanges. The proximal phalanges differ from those of the manus in having more inclined proximal articulations and a median tubercle (for extensor or ligament attachment?) on the proximodorsal surface. The ungual phalanx illustrated with the pes (Fig. 13) is relatively shallower and slightly less curved than those of the manus.

The overall pedal skeleton of *Alocodontulum*, like that of metacheiromyids (Matthew, 1918; Simpson, 1931), is generally similar to that of armadillos—much more so than to *Manis* (e.g., in relative proportions, form of the tarsals, and configuration of metapodial and phalangeal articular surfaces). We attribute this resemblance to similar functional constraints rather than phylogenetic proximity.

Measurements of hind limb elements of UM 93740 are listed in Table 3.

DISCUSSION

UM 93740, allocated to *Alocodontulum atopum*, is the oldest and most nearly complete epiocotheriid skeleton known. The skeleton represents an animal about the size of a small armadillo (*Euphractus* or *Dasypus*), with a head-body length of roughly 30 cm and a body weight estimated at approximately 1-2 kg (Table 4). It shows numerous fossorial specializations throughout, being characterized, especially in the limbs, by exaggerated crests and processes for muscle attachment. All limb segments are short relative to their diameters, and distal segments are markedly shortened relative to the humerus and femur (resulting in shorter out-lever arms, and consequently greater out-forces than in more generalized mammals). Differences between body masses predicted from different measurements in Table 4 reflect these differences of proportion in *Alocodontulum* relative to generalized mammals. Fossorial mammals display substantial convergence in limb osteology, and *Alocodontulum*, like other palaeonodons, corresponds closely in various respects to manids, dasypodids, and chrysochlorid insectivores in particular. The following inferences are based on this close correspondence.

The forelimb skeleton of *Alocodontulum* is particularly robust and constructed for powerful, though limited, movement. Muscles were typically attached relatively far from the joints they acted upon, thereby lengthening their lever arms and, hence, their power (for instance, the triceps attachment on the olecranon, or the distal insertions of deltoid, pectoralis major, and pronator teres). As in other diggers, the huge olecranon, projecting entepicondyle, and flaring lateral supracondylar ridge provided extensive areas of origin for the flexors and extensors of the wrist and digits. Both of these muscle groups (as well as pronator and supinator muscles, as indicated by the expanded distal radius) were apparently well developed, suggesting strong but slow and controlled motions. The olecranon may also have provided a relatively very distal insertion for latissimus dorsi or a part of this muscle, as in *Manis* and dasypodids (Humphry, 1869; Windle and Parsons, 1899a). In chrysochlorids, with a similar medial elbow region, latissimus dorsi inserts on the entepicondyle (Gasc et al., 1986). Distal insertion of latissimus dorsi would have enhanced its power as a retractor of the forelimb during digging. The deeply excavated proximomedial ulna in *Alocodontulum* may reflect an especially well-developed flexor digitorum profundus (as in *Euphractus* and *Tamandua*; Galton, 1870; Windle and Parsons, 1899a; Taylor, 1978). This is further suggested by the potential presence of a palmar sesamoid in the flexor tendon, and by the predominance of the manual digit III. All of these musculoskeletal traits indicate a capability for forceful digging. Eigenshape analysis of mammalian ungual phalanges indicates that the unguals of *Alocodontulum* correspond closely in shape with those of recent fossorial mammals (MacLeod and Rose, 1992).

Besides being adapted for strength, the forelimb anatomy of *Alocodontulum* also shows modifications for stability and restricted mobility, both of which would be advantageous in a digging animal. The prominent greater tubercle (and probably a long, overhanging acromion process, as in other palaeonodons) suggests limited shoulder mobility, or at least an emphasis on stability at this joint. Similarly, the structure of the elbow region—with its prominent medially-inflected olecranon, elongate entepicondyle, and broad, shallow trochlea—not only confined extension at the elbow to no more than about 130°, but probably also limited lateral mobility of the forearm (as in chrysochlorids, which are generally similar in this area; Puttick and Jarvis, 1977). Nonetheless, the sellar semilunar notch in *Alocodontulum* may have allowed the ulna to rock on the trochlea, resulting in a small degree of supination of the forearm. But supination seems to have been impossible at the proximal radioulnar joint, which must have been essentially fixed since this contact is nearly flat. Therefore, the well-developed pronator and supinator muscles presumably acted more to stabilize the forearm, or to move radius and ulna as a unit relative to the humerus, than to rotate the radius. [Despite a virtually flat radioulnar joint in most armadillos, however, Galton (1870) reported that limited supination

was possible. Perhaps this, too, results from greater freedom at the humeroulnar joint.] The distinct facets on the distal radius for scaphoid and lunar are possibly related to stability of the wrist.

Specializations for restricted mobility are particularly evident in the manus. The metacarpophalangeal and proximal interphalangeal articular surfaces appear to have substantially limited the degree of extension (and even flexion) at these joints. The specialized metacarpophalangeal joint of digit III prohibited hyperextension of the proximal phalanx, foreshadowing the situation in Oligocene *Xenocranium*, in which these two elements are synostosed (Rose and Emry, 1983). In contrast, the distal interphalangeal joints allowed a considerable range of flexion-extension of the ungual phalanges.

The hind limb skeleton of *Alocodontulum* is more generalized than that of the forelimb, but certain modifications may be associated with fossorial habits. The large peroneal processes on metatarsals I and V, and on the calcaneus, are suggestive of well-developed peroneal muscles associated with a capacity for powerful eversion, which would have been advantageous if *Alocodontulum* employed its hind limbs to brace itself while digging or to kick loose dirt from a burrow (as in *Chlamyphorus*: Rood, 1970). The distal tibiofibular joint was somewhat stabilized by the presence of a syndesmosis, but less so than in palaeonodons in which this joint was synostosed (*Xenocranium*, *Dipassalus*; Rose and Emry, 1983; Rose et al., 1991).

The vertebral column, though robust, does not show obvious specializations indicative of fossorial habits, such as fused cervical vertebrae. Noteworthy, however, are the thick spinous processes and enlarged metapophyses, which are almost even with the spinous processes, on the distal thoracic and lumbar vertebrae. These processes are reminiscent of those of manids and armadillos; in the latter they help to support the dermal armor. If palaeonodons had dermal armor, however, it is more likely to have been scaly (as in pangolins) than bony, since no bony scutes have ever been found with a palaeonodont.

Alocodontulum is the most fossorially adapted mammal known from the early Eocene of North America. It was probably armadillo-like in being generally terrestrial (not obviously subterranean) but a very proficient burrower. To the extent that they can be compared, *Alocodontulum* was postcranially more specialized for fossorial habits than its contemporary *Palaeonodon* (e.g., in having a shorter humerus relative to its distal breadth, in having a relatively longer, more ellipsoid humeral head, in having a longer deltopectoral crest, and in having relatively shorter and broader metacarpals). The olecranon is relatively longer and the radius relatively shorter than in middle Eocene *Metacheiromys* (complete, associated forelimb bones are not known for *Palaeonodon*). Despite these postcranial specializations, *Alocodontulum* was more conservative dentally than Eocene metacheiromyids.

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