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SKELETON OF *BRACHIANODON WESTORUM*, A NEW MIDDLE EOCENE METACHEIROMYID (MAMMALIA, PALAEANODONTA) FROM THE EARLY BRIDGERIAN (BRIDGER A) OF THE SOUTHERN GREEN RIVER BASIN, WYOMING

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Abstract—A new genus and species of metacheiromyid palaeanodont, *Brachianodon westorum*, is described, based on a nearly complete skeleton from the early Bridgerian (Bridger A) middle Eocene of southwestern Wyoming. *Brachianodon* has a number of primitive *Palaeanodon*-like characteristics including retention of five postcanine teeth, mediolateral compression of the humeral head, and anteroposterior compression of the distal tibia. *Brachianodon* differs from older *Palaeanodon* and from contemporary *Metacheiromys* in retaining enamel on postcanine teeth, in having more complex postcanine tooth morphology, in having a short tibia relative to femur length, and in having a very short astragalar neck and round astragalar head. Presence of *Brachianodon* in the early Bridgerian indicates that metacheiromyids were more diverse in the middle Eocene than previously recognized.

INTRODUCTION

The mammalian suborder Palaeanodonta is represented by a small North American radiation beginning in the late Paleocene (Matthew, 1918; Rose, 1978, 1979) and lasting through the early Oligocene (Douglass, 1905; Rose and Emry, 1983). Two families of palaeanodonts are recognized (Fig. 1): Epoicotheriidae, a group characterized by relatively small body size, relatively primitive dentitions, and highly specialized cranial and postcranial skeletons, especially in Oligocene taxa (Rose and Emry, 1983); and Metacheiromyidae, a radiation of larger bodied animals (larger compared to epoicotheriids), with less derived (although clearly specialized) postcrania, and a more specialized dentition (Simpson, 1931; Rose, 1978; Schoch, 1984; Rose et al., 1992).

Palaeanodonts are represented by relatively few taxa throughout their range. Three genera and three species are known from the late Paleocene, five genera and six species are known from the early Eocene, and three genera and possibly seven species are known from the early middle Eocene (Fig. 1). After the early middle Eocene palaeanodonts became quite rare, with only one tentative record from the Uintan and two genera and two species known from the latest Eocene-earliest Oligocene (Chadronian-Orellan).

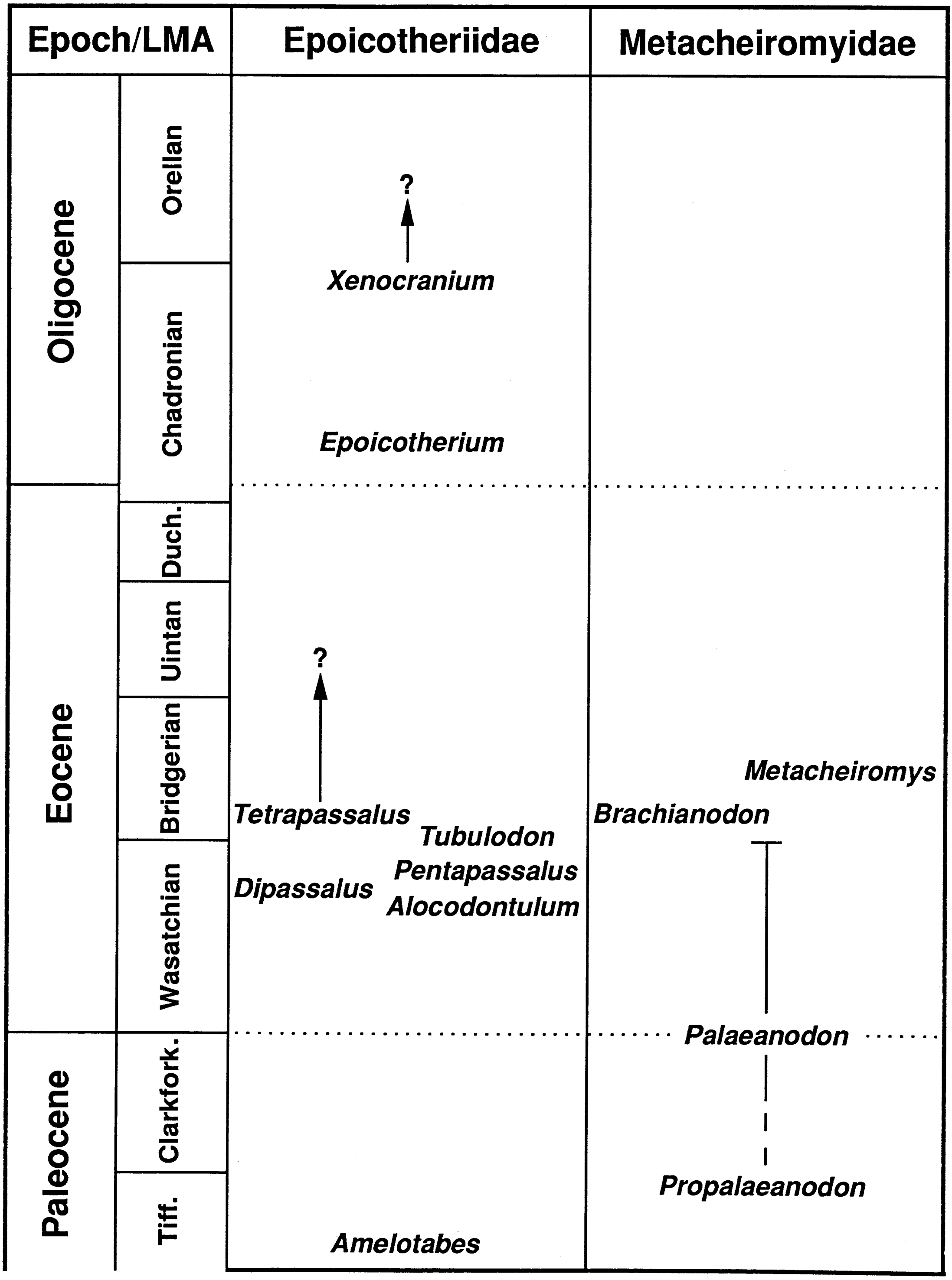

FIG. 1—Temporal distribution of palaeanodont families Epoicotheriidae and Metacheiromyidae from the Paleocene and Eocene of North America (adapted from Rose, 1978).

The general impression has been that palaeanodonts are rare in Paleogene faunas, but recent collecting efforts in the Wasatchian and early Bridgerian, and recent studies of postcrania (Rose and Emry, 1983, 1993; Rose, 1990; Rose et al., 1991, 1992) indicate that palaeanodonts are more common and diverse than previously thought. Dental remains of palaeanodonts are rare in the early Bridgerian of southwestern Wyoming, but postcranial elements have proven to be more common in collections made by parties from the University of Michigan, Albion College, and California State University at Sacramento. This is partially due to an improved ability to recognize palaeanodonts from postcrania, based on studies by Simpson (1931), Rose and Emry (1983, 1993), Schoch (1984), Gingerich (1989), and Rose et al. (1991, 1992).

The purpose of this paper is description of a new genus and species of palaeanodont from the early Bridgerian ("Bridger A"), which we consider in relation to other Bridgerian metacheiromyids.

ABBREVIATIONS

Institutional abbreviations used in this paper are as follows:

AMNH — American Museum of Natural History, New York
UM — University of Michigan Museum of Paleontology, Ann Arbor
YPM — Yale Peabody Museum, New Haven

SYSTEMATIC PALEONTOLOGY

Order INCERTAE SEDIS
Suborder PALAEANODONTA Matthew, 1918
Family Metacheiromyidae Wortman, 1903

Brachianodon, new genus

Type species.—Brachianodon westorum, new species

Included species.—Genotype only.

Diagnosis.—Differs from late Paleocene *Propalaeanodon*, to the extent these can be compared, in having all postcanine teeth single-rooted. Differs from late Paleocene and early Eocene *Palaeanodon* in having the medial buttress of the mandible less well developed, and in having a shorter tibia relative to femur length. Differs from middle Eocene *Metacheiromys* in retaining at least five postcanine teeth and in having a mediolaterally compressed humeral head. Differs from both *Palaeanodon* and *Metacheiromys* in having a complete enamel covering on postcanine teeth, in having a relatively short tibia, in having three distinct cuspules on lower postcanine teeth, and in having a very short astragalar neck, a round astragalar head, and a very short distal calcaneum.

Etymology.—brachys, Gr., short; *an*, Gr., without; *odon*, Gr., tooth; in reference to the relatively short tibia and the reduced dentition of this genus.

Discussion.—Several characteristics that distinguish *Brachianodon* from other metacheiromyids are similar to features in epoicotheriids. For example, the presence of postcanine teeth completely covered in enamel and retaining distinct cusp morphology (one specimen preserves a single, unworn tooth) is characteristic of epoicotheriids (see below). However, few specimens of metacheiromyids preserve teeth at all, and of these, few if any have unworn teeth. Rose (1978, 1979) stated that metacheiromyids apparently lacked enamel on postcanine teeth, but noted that verification might require sectioning and microscopic study. Also, *Dipassalus* *oryctes*, a recently described epoicotheriid(?) from the Wind River Basin (Rose et al., 1991) either had very thin postcanine enamel or lacked enamel completely. Guthrie (1967) noted that the epoicotheriid *Pentapassalus woodi* lacked enamel on postcanine teeth.

The presence of cuspules on postcanine teeth documented here suggests that *Brachianodon* may share a closer relationship with epoicotheriids than with metacheiromyids. However, the arrangement of cuspules on the postcanine teeth of *Brachianodon* does not resemble that of any known epoicotheriid and it is not clear how a "triconodont" metacheiromyid cusp pattern should be compared to cusps on generalized eutherian molars: possibly the small anterior cuspule in *Brachianodon* is homologous to the paraconid, the larger central cuspule is homologous to the protoconid, and the small posterior cuspule is homologous to the metaconid on the trigonid of a typical eutherian.

Brachianodon shares dental characteristics with metacheiromyids that are derived for the family. These include: postcanine teeth separated by diastemata (some epoicotheriids share this feature but their diastemata are usually much shorter); little or no differentiation in postcanine tooth size; tooth alveoli that are much larger in diameter than the teeth they contain (this characteristic is also present in the middle Eocene epoicotheriid *Tetrapassalus*); and a postcanine tooth row that does not extend posteriorly to the base of the ascending ramus (postcanine teeth extend to the back of the horizontal ramus in all epoicotheriids except *Dipassalus*, see Rose et al., 1991).

Postcranially, *Brachianodon*, resembles both metacheiromyids and primitive epoicotheriids. Primitive epoicotheriids (where known) do not share the striking fossorial adaptations exhibited in the derived Oligocene genera *Epoicotherium* and *Xenocranium* (Rose and Emry, 1983), but instead resemble metacheiromyids quite closely (Gazin, 1952; Rose, 1978; Rose et al., 1992). Differentiation of primitive epoicotheriids and metacheiromyids can be difficult, but, on balance, *Brachianodon* seems somewhat more metacheiromyid-like than epoicotheriid-like.

Brachianodon westorum, new species

Holotype.—UM 98743, including cranial fragments, left and right dentaries, and much of the postcranial skeleton from UM locality BB-7 in the NE¼, Section 24, T20N, R115W, Roberson Creek Quadrangle, Lincoln County, Wyoming.

Referred specimen.—UM 99720, right dentary with last postcanine tooth from UM locality BB-17.

Diagnosis.—As for the genus.

Age and Horizon.—BB-7 and BB-17 are both in the early middle Eocene, Bridgerian faunal zone Br-1, in lithostratigraphic interval A of the Bridger Formation ("Bridger A"), southern Green River Basin, Wyoming.

Etymology.—Named for Robert M. West and his son Christopher M. West, in recognition of the former's diverse contributions to our understanding of Eocene mammals, and the latter's many discoveries of important Bridgerian specimens. Chris West found the type specimen of *Brachianodon westorum* in 1991.

Description.—Detailed descriptions of the skull and dentition, axial skeleton, forelimb skeleton, and hind limb skeleton are provided in following sections of this paper.

SKULL AND DENTITION

Skull—Remains of the skull and dentition are known in two specimens, UM 98743 and 99720. These are all fragmentary. Close examination of broken basicranial pieces of UM 98743 suggests that *Brachianodon*, like *Palaeanodon*, may have lacked a completely ossified auditory bulla (Matthew, 1918), although the nature of the remains prevent certain determina-

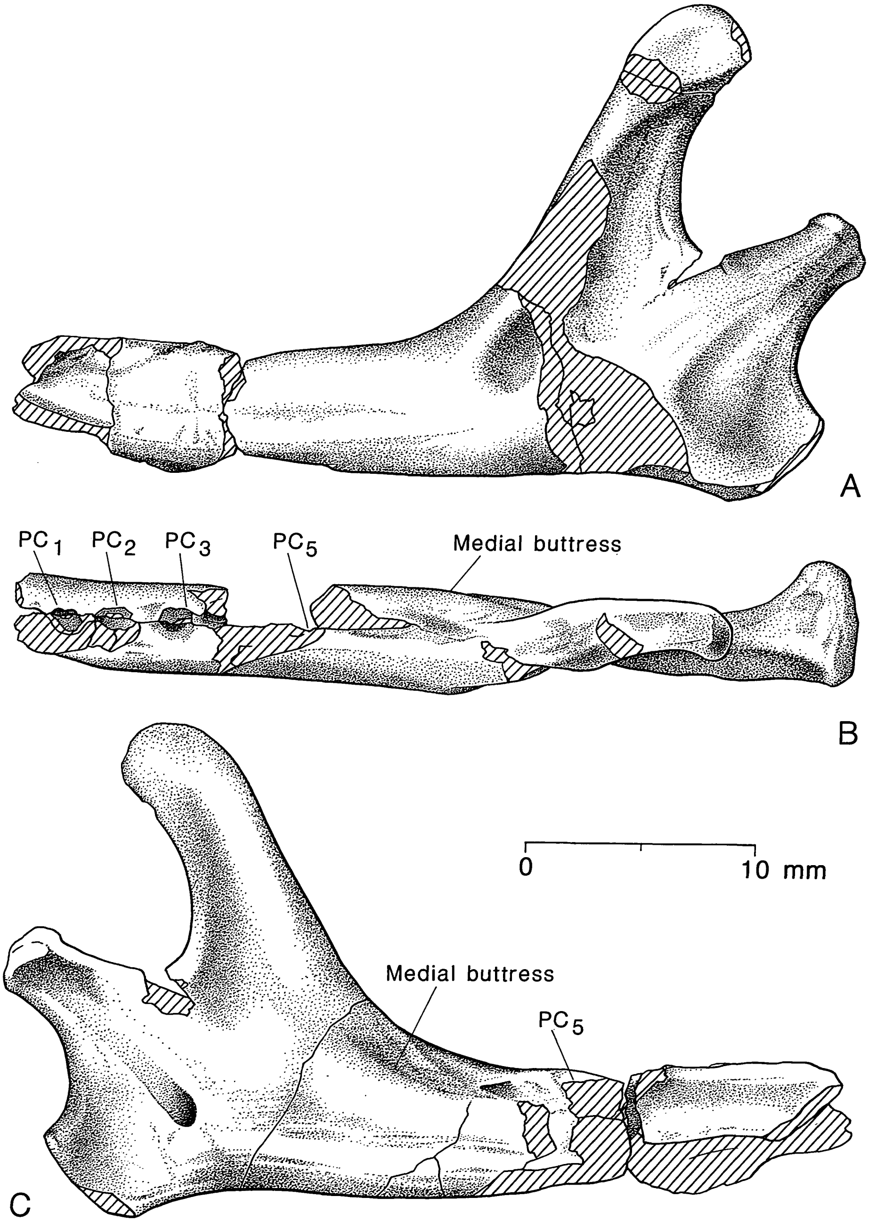

FIG. 2—*Brachianodon westorum*, UM 98743 (holotype), left dentary. A-C, lateral, occlusal, and medial views. This dentary preserves alveoli or parts of alveoli for four postcanine teeth, interpreted as $PC_{1\text{-}3}$ and PC_5, but no evidence of a canine alveolus. Medial buttress is weakly developed on the dentary of *Brachianodon*. Cross-hatching indicates broken surfaces in these drawings and in subsequent figures.

tion. *Metacheiromys* and all known epoicotheriids have a complete bony covering over the middle ear (Gazin, 1952; Rose, 1978; Simpson, 1931). This structure expands into the squamosal region of the posterior zygomatic arch in Oligocene epoicotheriids (Colbert, 1942; Rose and Emry, 1983).

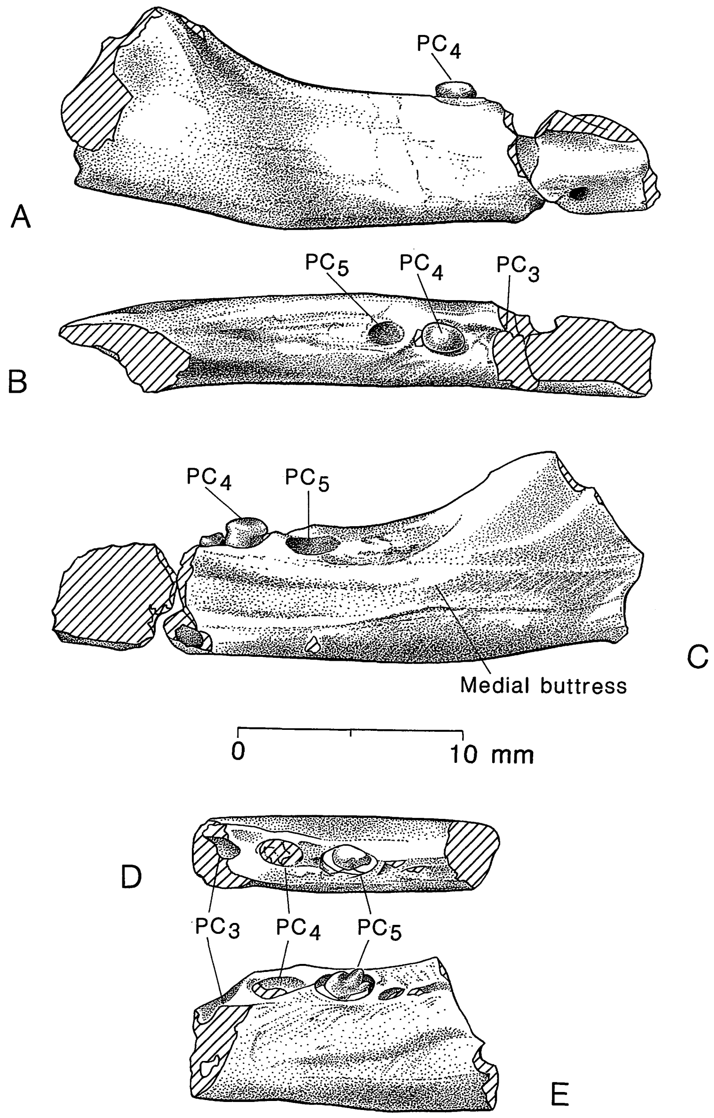

FIG. 3—*Brachianodon westorum*, right dentaries. A-C, UM 98743 (holotype) in lateral, occlusal, and medial views. This specimen preserves alveoli or parts of alveoli for three postcanine teeth, interpreted as PC$_{3-5}$, and a worn but intact crown interpreted as PC$_4$. D-E, UM 99720 in occlusal and medial views. This specimen preserves alveoli or parts of alveoli for three postcanine teeth, interpreted as PC$_{3-5}$, and an unworn crown of PC$_5$. Note distinct cusps preserved on crown of this tooth.

Dentaries—The dentaries of UM 98743 (Figs. 2, 3A-C) are somewhat broken, but are well enough preserved to show that *Brachianodon* had at least five postcanine teeth, as is true of *Palaeanodon*. There is no clear evidence of a canine alveolus in front of or beneath the alveolus for the most anterior postcanine tooth (here called PC$_1$), and it is possible that one or more postcanines preceded PC$_1$ in *Brachianodon*. Dentaries of *Brachianodon* have a medial buttress like that of other palaeanodonts, but this is less robust, relatively, than in *Palaeanodon*,

TABLE 1—Measurements of teeth and dentaries of *Brachianodon westorum*. PC$_{1\text{-}5}$ are postcanine teeth of uncertain homology. All measurements in mm.

		Left	Right
UM 98743 (holotype)			
PC$_4$	Crown length	—	1.8
	Width	—	1.2
Dentary	Depth behind PC$_5$	—	6.0
	Thickness behind PC$_5$	4.2	3.9
UM 99720			
PC$_5$	Crown length	—	1.6
	Width	—	1.1
Dentary	Depth behind PC$_5$	—	6.3
	Thickness behind PC$_5$	—	3.2

and it is more like the medial buttress seen in *Metacheiromys*. The buttress extends forward to encompass the last two postcanines in UM 98743 and UM 99720 (Fig. 3D,E), but it is less well developed in the latter specimen. Like all metacheiromyids, alveoli are noticeably larger than the teeth they contain, and all alveoli are separated by distinct diastemata. Judging by the size of alveoli, there was little size differentiation among postcanine teeth.

UM 99720 (Fig. 3D,E) is a partial dentary preserving three alveoli and the intact crown of the last postcanine tooth. The crown is completely covered in enamel and has three well developed cuspules. *Palaeanodon* and *Metacheiromys* apparently either lacked enamel or had a very thin veneer of enamel on the tip of the tooth that was rapidly worn away. There is no evidence of cusps or cuspules on the teeth of *Palaeanodon* or *Metacheiromys*. Epoicotheriids (where known) evidently had a well developed cusp pattern homologous with that of other primitive eutherians (Rose, 1978). *Brachianodon* has a single central cusp with a small anterior cuspule and a small posterior cuspule set off slightly from the posterior flank of the central cusp. These cuspules are aligned mesiodistally along the tooth with the anterior cuspule being positioned slightly medial to the other two. *Brachianodon* differs from both metacheiromyids and epoicotheriids in these tooth features.

Measurements of teeth and dentaries of *Brachianodon westorum* are listed in Table 1.

AXIAL SKELETON

Vertebral column—UM 98743 preserves a substantial portion of the postcranial skeleton of *Brachianodon westorum*, which is described here and compared to postcranial remains of other palaeanodonts. Comparisons are made with described skeletons of *Palaeanodon* (Matthew, 1918), *Metacheiromys* (Simpson, 1931), *Pentapassalus* (Gazin, 1952), *Dipassalus* (Rose et al., 1991), and *Alocodontulum* (Rose et al., 1992), as well as with other undescribed Bridgerian palaeanodont skeletons in the University of Michigan collections.

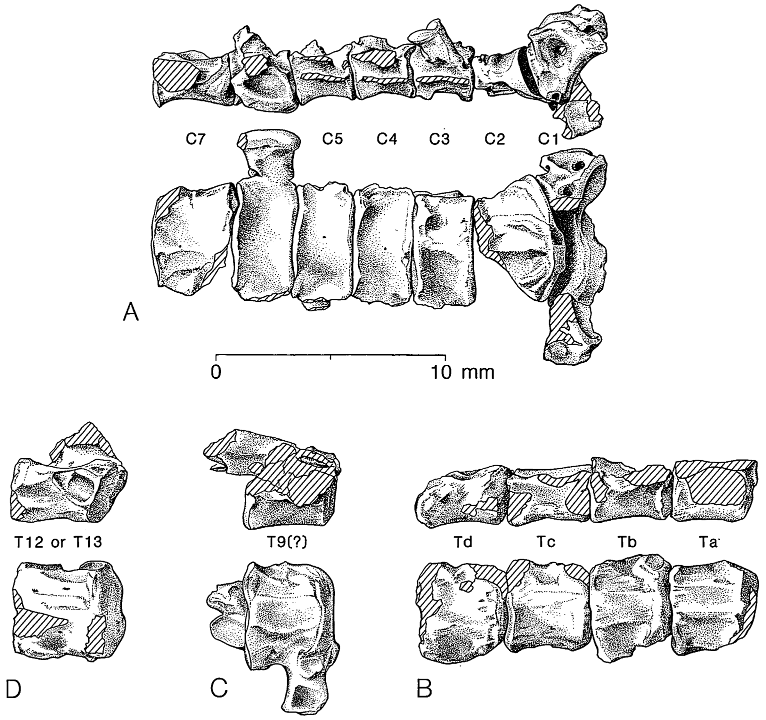

FIG. 4—*Brachianodon westorum*, UM 98743 (holotype), cervical and thoracic vertebrae in right lateral and ventral views. A, C1-C7. All seven centra are separate; none of the cervicals is fused to another. B, series of four anterior thoracics of uncertain position. C, T9(?). D, T12 or T13.

The vertebral column of *Brachianodon westorum* is represented by all seven cervicals, six thoracics, four lumbars, four sacrals, and eight caudal vertebrae. All of these vertebrae are broken and most are represented by centra only.

The atlas (C1 in Fig. 4A) is missing its ventral arch but it does preserve the dorsal (neural) arch and portions of both transverse processes. The neural arch is anteroposteriorly narrow ventrally, broadening somewhat dorsally. There is a relatively robust, bifurcate anterior process developed centrally on the dorsal arch. This process is relatively larger and more robust than that described for *Metacheiromys* (Simpson, 1931), but is smaller than in *Dasypus*. The neural arch projects farther dorsally than in either *Dasypus* or *Metacheiromys*, consequently the neural canal is relatively deeper dorsoventrally.

As in *Metacheiromys* (Simpson, 1931), the posterior vertebral foramina are positioned above and lateral to the articular facets for the axis (not above and medial as in *Dasypus*). The posterior foramina are connected to anterior vertebral foramina that open just anterior to the ventral roots of the neural arch. Unlike both *Metacheiromys* and *Dasypus*, *Brachianodon* lacks dorsolateral foramina. Dorsolateral foramina are continuous with the anterior foramina in *Metacheiromys* and *Dasypus*.

The other six cervical vertebrae (Fig. 4A) are represented only by centra (except for C6 which has its right transverse process in place). As in all other known metacheiromyids, the cervicals of *Brachianodon* are unfused. The centra are short anteroposteriorly, transversely broad, and dorsoventrally compressed (but not as dramatically as in *Dasypus*). Like *Alocodontulum*, all cervical centra are approximately the same length, except C7 which is somewhat longer (Rose et al., 1992). The transverse process of C6 arises from the anterior

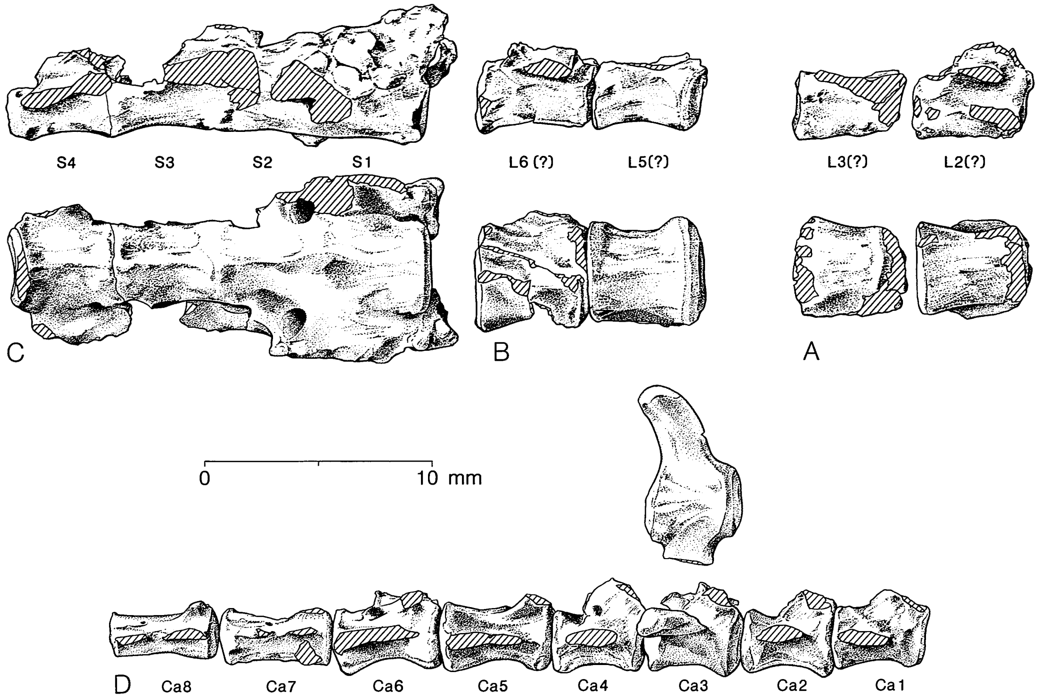

FIG. 5—***Brachianodon westorum***, UM 98743 (holotype), lumbar, sacral, and caudal vertebrae in right lateral and ventral views. A, upper lumbars, L2(?) and L3(?). B, lower lumbars, L5(?) and L6(?). C, sacrum. D, Ca1-Ca8. Note fusion of four vertebrae to form sacrum: two true sacrals articulating with left and right ilia, and two "pseudosacrals" (sacralized caudals).

portion of the centrum and is moderately down-turned (ventrally). The vertebral foramen is positioned lateral to the centrum, not dorsally as in *Dasypus*.

Thoracic vertebrae of *Brachianodon* are represented by six centra (Fig. 4B-D), four from the upper thoracic region, and two lower thoracics (perhaps T9 and T12 or T13). The upper thoracic vertebral centra are relatively short anteroposteriorly (but not as short as the cervicals), and not particularly wide transversely. The lower thoracic centra are somewhat longer and broader than the upper thoracics. None of the thoracic centra are as compressed dorsoventrally as the cervicals. T9? preserves its left transverse process. As in *Alocodontulum* (Rose et al., 1992), the transverse process originates from the anterior part of the centrum and has an oval, concave facet for a rib tubercle on its dorsolateral surface. Demifacets for rib heads are not well defined in the upper thoracics, but are distinct concavities on the two lower thoracics (Fig. 4D).

UM 98743 preserves four lumbar vertebral centra (Fig. 5A,B). The centra increase in size and robustness caudally. As with the thoracics, transverse processes originate from the anterior portion of the centra. Centra are less compressed dorsoventrally than thoracics but few other details can be noted given the poor nature of preservation of these vertebrae.

The sacrum of *Brachianodon* (Fig. 5C) consisted of four fused vertebrae, two true sacrals and two "pseudosacrals" (sacralized caudals), as in *Palaeanodon* and *Metacheiromys* (the type specimen of *Metacheiromys tatusia* apparently had only three sacral vertebrae; see Simpson, 1931). *Alocodontulum* has three fused sacral vertebrae including just one pseudosacral (Rose et al., 1992). The sacroiliac articulation in *Brachianodon* is elongate and encompasses the first

TABLE 2—Measurements of vertebral centra of *Brachianodon westorum*, UM 98743. All measurements in mm.

		Length	Max. trans. diameter	Dorsoventral diameter
Cervicals	C3	6.7	12.1	5.3
	C4	6.6	12.8	5.6
	C5	6.4	12.1	6.1
	C6	6.3	12.3	5.9
	C7	9.0	11.1	5.5
Thoracics	Ta	8.3	10.1	---
	Tb	8.7	9.1	---
	Tc	7.8*	9.1*	4.9
	Td	7.8	9.4	4.4
	T9(?)	7.8	10.2	---
	T12 or 13	9.4	10.4	---
Lumbars	L2(?)	11.2	11.2	---
	L3(?)	12.7	11.4	---
	L5(?)	13.4	12.3	---
	L6(?)	12.6	12.2	---
Sacrum	S1-4	45.0	21.4	---
Caudals	Ca1	10.1	9.2	7.0
	Ca2	10.5	8.6	6.8
	Ca3	10.3	8.3	7.3
	Ca4	10.4	9.0	7.2
	Ca5	12.5	9.4	7.7
	Ca6	11.7	8.5	7.0
	Ca7	12.4	7.4	6.1
	Ca8	11.7	7.0	5.9

*Approximate.

and second sacrals as in metacheiromyids. This articular surface is restricted to the first sacral in primitive epoicotheriids (Rose et al., 1992).

Eight caudal vertebrae are preserved in UM 98743 (Fig. 5D), but clearly there are many missing from the end of the tail. Preserved centra increase in length caudally, but decrease in height (dorsoventrally). The first four caudal vertebrae possess robust, somewhat caudally-directed transverse processes (one is preserved in place on Ca3). Transverse processes originate from the middle of centra, unlike those of the presacral vertebrae. Ca5-6 appear to have had relatively large transverse processes that were more dorsoventrally flattened, but perhaps broader anteroposteriorly, than those of Ca1-4. Posterior to Ca8, all caudal vertebral processes are evidently reduced or absent.

Measurements of vertebrae of *Brachianodon westorum* are listed in Table 2.

Ribs and sternum—Rib and sternal fragments are generally unremarkable. They resemble rib and sternal fragments described for *Metacheiromys* (Simpson, 1931) and *Alocodontulum*

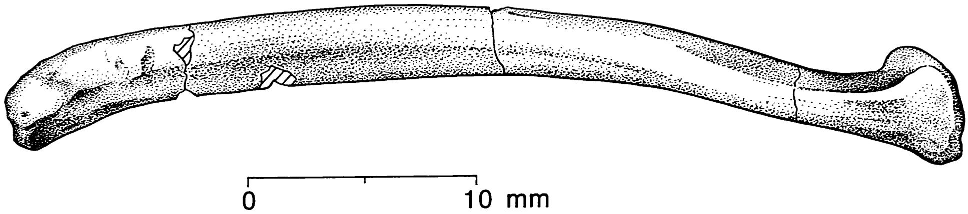

FIG. 6—*Brachianodon westorum*, UM 98743 (holotype), right clavicle in anterior view.

(Rose et al., 1992) quite closely. There is no evidence to suggest that *Brachianodon* had ossified sternal ribs as in xenarthrans.

FORELIMB SKELETON

Scapula—Scapular fragments of UM 98743 indicate that *Brachianodon* is similar in scapular morphology to *Metacheiromys* (Simpson, 1931). The scapular spine is prominent, but there is no evidence to suggest the presence of a secondary spine as in most xenarthrans (Rose and Emry, 1993). As in *Patriomanis* (Emry, 1970), *Brachianodon* appears to have had a broad, elevated, caudal scapular border). The acromion is robust and must have overhung the humeral head. It is two-pronged as in *Metacheiromys* (Simpson, 1931).

Clavicle—The clavicle (Fig. 6) is somewhat sigmoidal mediolaterally and is slender and delicately built. It is very long, being 80% of the length of the humerus (see Table 3 for forelimb measurements). In *Metacheiromys* the clavicle is relatively shorter (65% of humerus length), but is also lightly built and slender (Simpson, 1931). Clavicles remain unknown or undescribed for other palaeanodonts.

Humerus—The humerus of *Brachianodon* is quite similar to that in other palaeanodonts (Fig. 7). The humeral head is mediolaterally compressed as in *Palaeanodon*, but not as compressed as in most epoicotheriids. *Metacheiromys* has a less compressed, more ovoid to round humeral head. *Palaeanodon*, *Metacheiromys*, and the epoicotheriid *Alocodontulum* have a robust deltopectoral crest that flares distally toward the capitulum (laterally). The deltopectoral crest in *Brachianodon* is relatively less robust and lacks distal flaring. The distal portion does not turn toward the capitulum but continues medially toward the trochlea. A distinctive feature of all palaeanodonts is a greatly expanded, flaring supinator crest. *Brachianodon* has an enlarged supinator crest, but it is more flattened and not as posteriorly expanded as that typical of *Palaeanodon* and *Metacheiromys*.

Ulna and radius—Parts of both ulnae are preserved, with the right ulna being the more complete (Fig. 8A,B). It has the large medially-inflected olecranon typical of metacheiromyids. The left ulna is notable in preserving the distal end with the styloid process intact. The ulna of *Brachianodon* generally resembles that of *Metacheiromys* more closely than *Palaeanodon*. The radial articular surface is oriented transversely, and it is separated from the trochlear surface by a small but distinct ridge. In *Palaeanodon* the radial articulation is oriented more anteroposteriorly and it is more continuous with the trochlea.

The proximal radius of *Brachianodon* (Fig. 9A,B) is similar to that of other palaeanodonts in having an anteroposteriorly compressed head and a deep concavity for the capitulum. The distal radius of *Brachianodon* (Fig. 9C-E) is less expanded medially than that of *Palaeanodon* and *Metacheiromys*. *Brachianodon* has a distinct anterolateral crest on the distal radius, a feature also exhibited in *Pentapassalus* (Rose et al., 1992) and *Palaeanodon*. This crest is more centrally placed in *Palaeanodon* and relatively more elevated from the radial shaft.

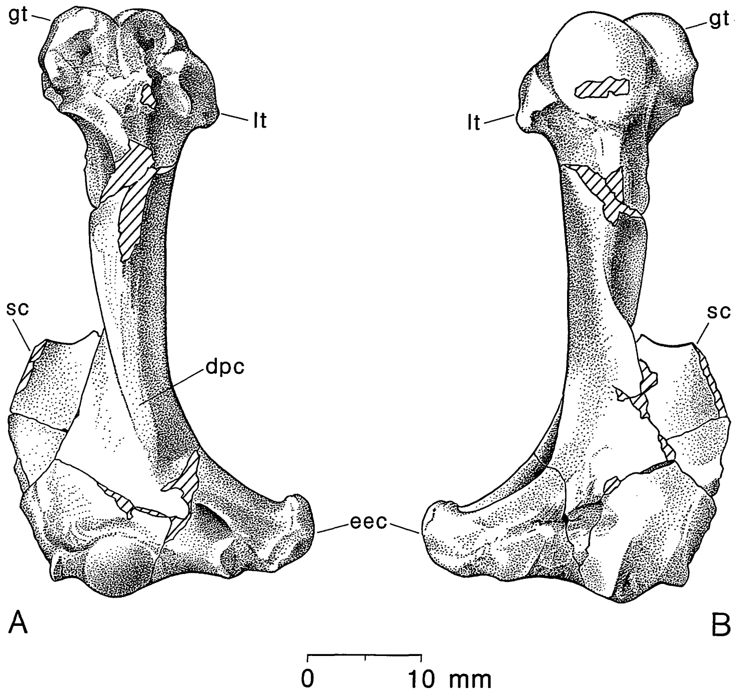

FIG. 7—*Brachianodon westorum*, UM 98743 (holotype), right humerus. A-B, anterior and posterior views. Abbreviations: *dpc*, deltopectoral crest; *eec*, entepicondyle; *gt*, greater tuberosity; *lt*, lesser tuberosity; *sc*, supinator crest.

Metacheiromys has a much lower anterior crest that angles laterally and is positioned farther laterally than in any other known palaeanodont.

All three metacheiromyids (*Palaeanodon*, *Brachianodon*, and *Metacheiromys*) have a distinct tubercle on the anterior radial crest positioned much farther distally (just anterior to the distal articular surface, Fig. 9D,E) than a similar tubercle in *Alocodontulum* and *Pentapassalus* (Gazin, 1952; Rose et al., 1992). The distal radial articular surface for the lunar and scaphoid resembles that of *Alocodontulum* and *Palaeanodon*, in having the two facets weakly differentiated with the lunar facet relatively larger anteroposteriorly (Fig. 9D). *Metacheiromys* differs from these genera in having confluent lunar and scaphoid facets, with the scaphoid facet being relatively larger and more convex.

Carpus—UM 98743 preserves much of a right carpus of *Brachianodon* including all bones except the trapezoid. The scaphoid (Fig. 10A-D) is a separate bone from the lunar, as in all known palaeanodonts and extant xenarthrans: it is not fused to the lunar as in *Manis* (Flower, 1885), and is not expanded medially as in extant pangolins. The scaphoid is dorsoplantarly elongate and proximodistally narrow. A convex radial facet extends nearly to the dorsal margin of the proximal end. The palmar surface consists of two subequal-sized processes separated by a groove or notch as in *Metacheiromys* (Simpson, 1931). This notch is also found in *Dasypus*, where it provides the medial articular surface for an enlarged palmar sesamoid (falciform) bone. Palmar sesamoids are present in many xenarthrans and in pangolins (Flower, 1885; Galton, 1870; Windle and Parsons, 1899). A palmar sesamoid is present in the Oligocene epoicotheriid *Xenocranium* (Rose and Emry, 1983) and it was probably present in *Alocodontulum* as well (Rose et al., 1992). Suggested presence of a palmar sesamoid in

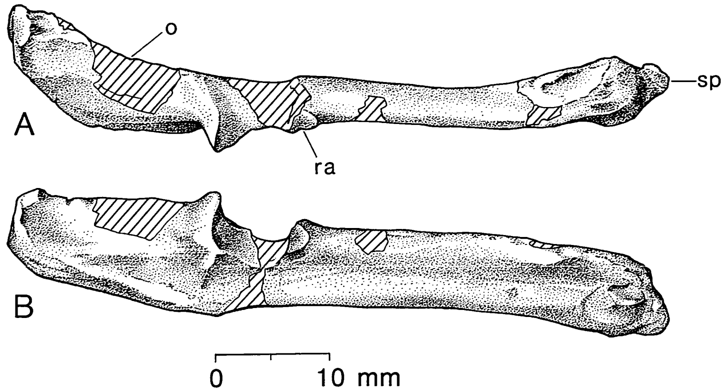

FIG. 8—*Brachianodon westorum*, UM 98743 (holotype), ulna. A-B, right ulna in anterior and lateral views. Abbreviations: *o*, olecranon; *ra*, radial facet; *sp*, styloid process (reversed from left side).

Brachianodon is, therefore, not surprising as this characteristic may be common to all palaeanodonts.

The distal side of the scaphoid is quite complex, but resembles *Metacheiromys* in most details. There is a concave dorsal facet for the trapezoid that tapers palmarly to a small ridge that separates the dorsal facet from another concave, palmar trapezoid facet. This resembles the condition in extant armadillos, pangolins, and *Myrmecophaga* (*Tamandua* and *Cyclopes* lack a scaphoid-trapezoid contact). Just medial to the ridge is a distinct flattened facet for the trapezium. The trapezial articulation extends palmarly from this flat facet along a ridge that forms the medial margin of the palmar trapezoid facet. Laterally, the scaphoid has a dorsopalmarly elongate and relatively narrow facet for the lunar, and a small magnum facet palmar to the lunar facet. This magnum facet is less continuous with the dorsal trapezoid facet than in *Metacheiromys* and instead is separated by a sharp angulation.

The lunar (Fig. 10E-G) is very similar to that described for *Alocodontulum* (Rose et al., 1992). It is elongated dorsopalmarly and narrow mediolaterally. On the proximal end, the convex radial facet extends to the dorsal margin as in *Alocodontulum* and *Pentapassalus*. Medially there is an elongated facet for the scaphoid. On the lateral side is a projecting palmar process that provides an articular surface for the palmar extension of the unciform (hamate). Dorsal to this process is a flattened facet for the cuneiform (triquetrum). The distal surface has a convex dorsal aspect that grades into a palmar concave surface and articulates with the magnum. The distal surface is similar to that of *Alocodontulum* (Rose et al., 1992), *Metacheiromys* (Simpson, 1931), and *Pentapassalus* (Gazin, 1952), except that the two magnum articular facets are not as sharply separated as in those genera. There is a small facet for a dorsal portion of the unciform situated between the magnum and cuneiform facets as in *Metacheiromys*. The palmar portion of the lunar consists of a rounded articular surface for the palmar sesamoid. This morphology is also found in *Alocodontulum*, *Metacheiromys*, and *Xenocranium*.

The cuneiform (Fig. 10H,I) is a relatively small bone resembling that of other known palaeanodonts. The proximal surface has distinct, elongate facets for the pisiform (more palmar) and ulna. These facets are separated by a sharp angulation as in *Alocodontulum*. There is a distinct, flattened facet for the lunar on a small medial projection, and a small elongated facet for the fifth metacarpal on the lateral side (as in *Euphractus*, but unlike *Dasypus* where the unciform provides the only articulation with Mc V). Distally, the unciform facet of the cuneiform forms an undulating surface with a concave medial portion that grades into a convex ridge lateropalmarly.

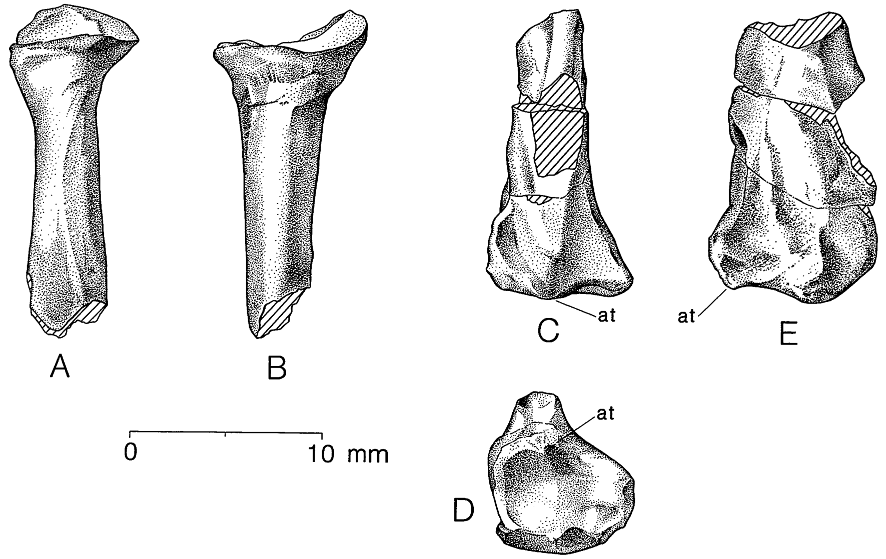

FIG. 9—*Brachianodon westorum*, UM 98743 (holotype), radius. A-B, left proximal radius in medial and anterior views. C-E, right distal radius in anterior, distal, and lateral views. Abbreviation: *at*, anterior tubercle.

The pisiform of *Brachianodon* (Fig. 10J-L) resembles that described for *Metacheiromys* (Simpson, 1931). It is L-shaped with a long palmar projection and a shorter cuneiform-ulnar projection. There is an elongate, flat facet for the cuneiform along the dorsodistal surface. Just proximal and lateral to the cuneiform facet is a rounded, concave facet for the ulna. The pisiform articulates only with the cuneiform and ulna in *Brachianodon*, unlike *Cyclopes* and *Manis* where the pisiform has a broad contact with the unciform (*Dasypus* often has a small pisiform-unciform contact).

The unciform is a wedge-shaped, triangular bone with proximal, distal and medial surfaces (Fig. 11N-P). The unciform is relatively small as in extant armadillos, not enlarged as in anteaters, and it is not palmarly extended as in pangolins. The proximal surface is smoothly convex for articulation with the cuneiform. This articulation extends distally into dorsal (longer) and palmar (shorter) narrowing processes. The cuneiform articulation joins the facet for the magnum proximomedially. These two facets are separated by a very slight ridge. The magnum facet continues mesiodistally along the dorsal aspect of the unciform until it joins a small flat facet for the third metacarpal. The distal surface is divided dorsoplantarly by a faint ridge centrally. On either side of this ridge are dorsopalmarly concave facets for the fourth and fifth metacarpals. These two facets are continuous palmarly, terminating in a small palmar projection. As in *Metacheiromys*, a portion of the magnum facet may contact the distal lunar surface (Simpson, 1931).

The magnum (capitate) of *Brachianodon* (Fig. 11J-M) has rounded convex surfaces both proximally and distally, for the lunar and for the third metacarpal respectively. Proximally, the magnum contacts only the lunar as in armadillos (in anteaters there is a broad scaphoid contact with the magnum as well). The lateral side has a shallow, dorsopalmarly elongated, concave surface for articulation with the unciform, much as in *Pentapassalus* and *Metacheiromys*. There is a rounded concavity on the medial side for articulation with the second metacarpal (Fig. 11L). The dorsal surface forms a curving process that is concave distally. The concave surface forms the articular facet for the third metacarpal.

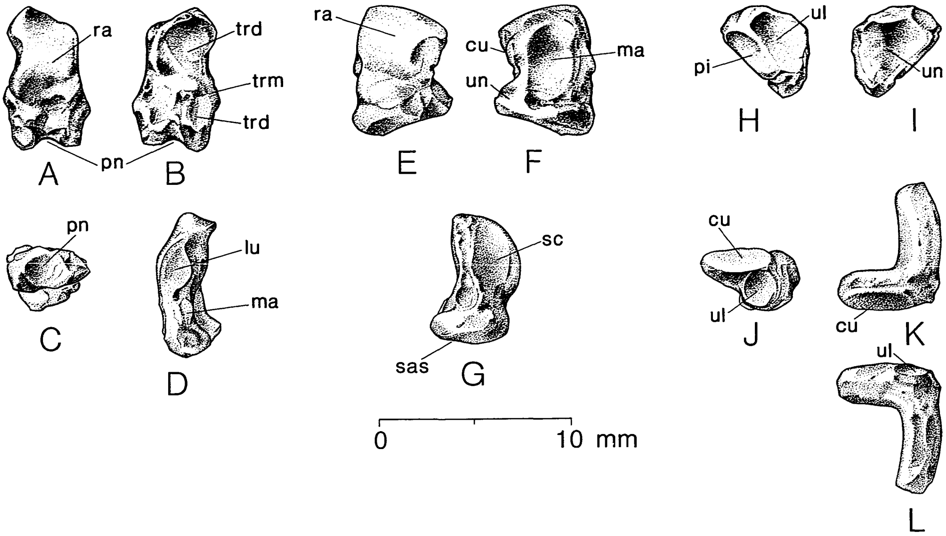

FIG. 10—*Brachianodon westorum*, UM 98743 (holotype), right proximal carpal row. A-D, scaphoid in proximal, distal, plantar, and lateral views. E-G, lunar in proximal, distal, and medial views. H-I, cuneiform in proximal and distal views. J-L, pisiform in dorsal, distal, and proximal views. Abbreviations: *cu*, cuneiform facet; *lu*, lunar facet; *ma*, magnum facet; *pi*, pisiform facet; *pn*, palmar notch; *ra*, radial facet; *sas*, sesamoid articular surface; *sc*, scaphoid facet; *trd*, trapezoid facet; *trm*, trapezium facet; *ul*, ulnar facet; *un*, unciform facet.

The trapezium, undescribed for other palaeanodonts, is preserved in *Brachianodon* (Fig. 11H,I). It is a small bone, elongate dorsopalmarly and narrow mediolaterally. On the lateral dorsal surface is a small, flat facet for articulation with the scaphoid. Continuing palmarly from this flat facet is a groove that articulates with the medial palmar ridge of the scaphoid (medial margin of the palmar trapezoid facet of the scaphoid). The distal end of the trapezium consists of two slightly concave facets, one facing directly distally and one angled distomedially (Fig. 11H). These facets are separated by a faint ridge. The distal facet is for the main articular surface of the first metacarpal. The distomedially angled facet is for the medial projection of the first metacarpal.

Manus—The first metacarpal, Mc I (Fig. 11F,G), is shorter than Mc IV (Fig. 11E), but nearly as broad. At the proximal end is a dorsopalmarly elongated, mediolaterally narrow, articular facet for the trapezium. This facet extends onto the dorsal aspect of the proximal end. On the medial portion of the proximal surface is a relatively large, proximally projecting process. This process has an articular facet for the trapezium along its lateral surface that is continuous with the proximal facet, but differentiated by a sharp angulation between the two. On the lateral side of the proximal end is an elongated cavity for a process of the second metacarpal. In distal view, the shaft of the first metacarpal is dorsopalmarly thick medially and relatively thin laterally. The distal end also shares this asymmetry with the medial side much thicker than the lateral side. The medial phalangeal facet is correspondingly larger than the lateral phalangeal facet. These facets are separated from each other by a very weak, low process.

The second metacarpal of *Brachianodon* is represented only by the distal end (Fig. 11A). Judging by the preserved portion, Mc II was somewhat less robust than Mc III but much larger than Mc I, Mc IV, or Mc V. In distal view the outline of Mc II is more irregular than that of Mc III, with a dorsopalmarly deep lateral margin that tapers to a more shallow medial margin.

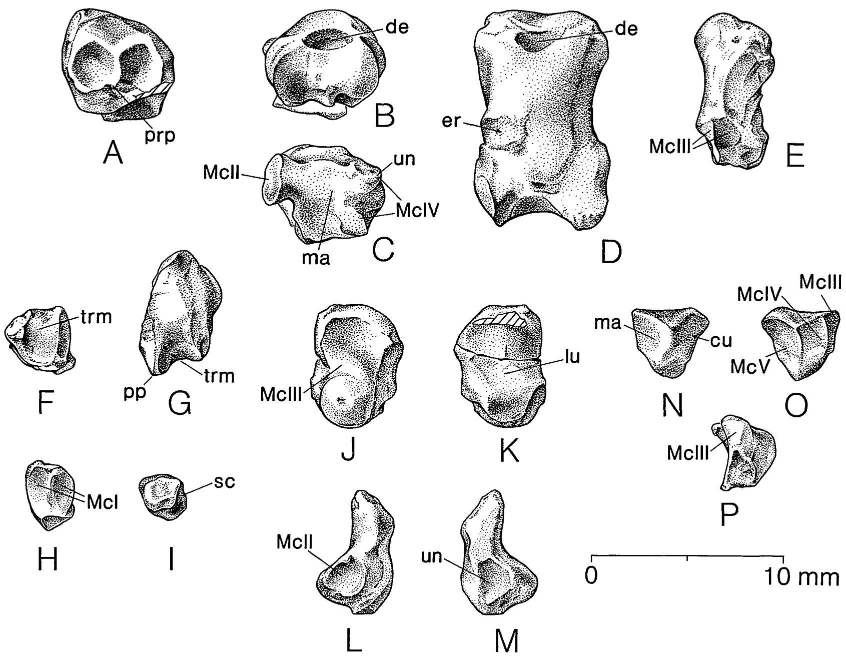

FIG. 11—*Brachianodon westorum*, UM 98743 (holotype), right distal carpal row and metacarpals. A, metacarpal II in distal view. B-D, metacarpal III in distal, proximal, and dorsal views. E, metacarpal IV in dorsal view. F-G, metacarpal I in proximal and dorsal views. H-I, trapezium in distal and dorsal views. J-M, magnum in proximal, distal, medial, and lateral views. N-P, unciform in proximal, distal, and medial views. Abbreviations: *cu*, cuneiform facet; *de*, dorsal excavation or pit for origin of dorsal ligament; *er*, extensor rugosity; *lu*, lunar facet; *ma*, magnum facet; *Mc I*, metacarpal I facet; *Mc II*, metacarpal II facet; *Mc III*, metacarpal III facet; *Mc IV*, metacarpal IV facet; *Mc V*, metacarpal V facet; *pp*, proximal process; *prp*, palmar process; *sc*, scaphoid facet; *trm*, trapezium facet; *un*, unciform facet.

The lateral half of the distal end has a short, cylindrical ridge dorsally and a relatively large concavity palmarly (larger than the phalangeal concavities of Mc III). The medial side has no ridge, but has a deeper concavity about the same size as the lateral one. The two phalangeal concavities are separated by a relatively robust ridge that terminates palmarly in a distinct, pointed process. The dorsal surface of the distal end of Mc II lacks the deep excavation present on Mc III.

The third metacarpal of *Brachianodon* (Fig. 11B-D) is very robust and relatively short and broad, as in most palaeanodonts. On the dorsomedial surface of the shaft is a distinct rugosity for insertion of a strong extensor carpi radialis tendon as in *Alocodontulum* (Rose et al., 1992). The proximal end is complex, with several articular surfaces. It is vaguely K-shaped. The articular surface for the magnum is convex proximally, with a gently rounded convex dorsal surface and a concave palmar surface. There is a well developed medial process extending from the dorsal aspect of the articular facet. On the medial face of this projection is a squared, flat facet for articulation with the second metacarpal. Laterally there are two projections, one dorsal (larger) and one palmar. Both are smaller than the medial process. On the palmar aspect of the dorsal process is a semilunar facet for the fourth metacarpal. On the proximal aspect of the dorsal projection is a small facet for the unciform.

The distal end of the third metacarpal is only slightly broader mediolaterally than it is deep. It is dominated by a transverse cylindrical articular surface. Dorsal to this surface is a deep

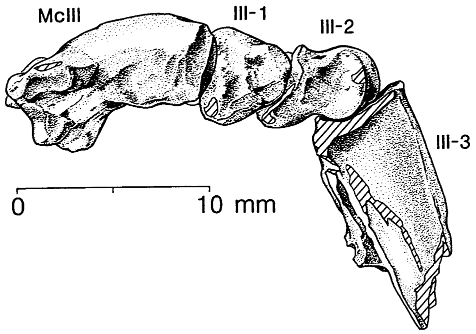

FIG. 12—*Brachianodon westorum*, UM 98743 (holotype), articulated metacarpal Mc III and proximal, medial, and distal phalanges of the enlarged middle digit of the right manus, right lateral view. Note large terminal phalanx forming the base for a much larger digging claw. Both left and right distal phalanges are preserved in UM 98743; both articulate well with the right phalanx III-2 shown here, and we are unable to be certain which belongs to the right and which to the left hand. Joint surfaces show that in life there was limited flexion between metacarpal III and manual phalanx III-1, little or no flexion between phalanges III-1 and III-2, and considerable flexion between phalanges III-2 and III-3 (through an angle of about 90°). Terminal phalanx III-3 could be extended straight out from III-2 in life; it is shown here in a position of maximum flexion.

central pit for origin of a dorsal ligament binding Mc III to more distal phalanges, probably III-3 especially (see discussion). Plantar to the cylindrical articular surface is a central process flanked medially and laterally by small phalangeal depressions. The central process interlocks with a corresponding concavity in the proximal phalanx.

Mc IV is illustrated in Fig. 11E. It articulates with the dorsal process of Mc III and also with the dorsal aspect of the palmar process of Mc III, projecting between the two processes. Articular facets for Mc V on the cuneiform and unciform show that *Brachianodon* retained a small fifth digit of the hand, but no bones of this digit are preserved.

The only ray of the manus for which phalanges can be certainly associated is right digit III. Right Mc III and proximal, medial, and distal phalanges III-1, III-2, and III-3 are shown in articulation in Figure 12. Phalanges III-1 and III-2 are short and broad, with substantial medial and lateral plantar processes for ligament and/or tendon insertions at each proximoplantar corner. Phalanx III-1 fits tightly onto the distal surface of Mc III, interlocking in a way that permits limited dorsal-ventral rotation but no other motion. Phalanx III-1 has what appears at first to be a pathological distal end, but this fits tightly against the proximal surface of phalanx III-2. The two phalanges are not fused, but no motion is possible at this joint. The middle phalanx is clearly longer than the proximal phalanx (Table 3), as in many xenarthrans and manids (Rose and Emry, 1993, p. 93). Lack of motion between phalanges III-1 and III-2, with the latter being longer, appears to characterize *Metacheiromys dasypus* as well, judging from Simpson's fig. 17B (Simpson, 1931). The distal end of III-2 has a well defined trochlea for articulation of distal phalanx III-3, permitting flexion of III-3 through an angular range of about 90°. The plantar surface of III-3 has medial and lateral pits for insertion of plantar ligaments, and a large central projection for insertion of a strong flexor tendon. Phalanx III-3 is covered with vascular impressions and it clearly bore a large digging claw in life.

Other manual or pedal phalanges are similar to those described by Simpson (1931) and Rose et al. (1992) for other palaeanodonts. Proximal and medial manual phalanges are characterized by being very short and broad. It is not possible to determine if any digit other than digit III had medial phalanges longer than proximal phalanges. Distal phalanges appear similar to those described for *Alocodontulum* (Rose et al., 1992). These are laterally compressed and modestly

TABLE 3—Measurements of forelimb elements of *Brachianodon westorum*, UM 98743. Lengths of long bones are measured from proximal to distal articular surfaces. All measurements in mm.

		Left	Right
Clavicle	Length	—	40.9
Humerus	Length (head to trochlea)	—	51.1
	Length of deltopectoral crest[1]	—	40.7
	Head, length	12.7	12.7
	Head, width	8.6	9.2
	Distal (epicondylar) breadth	22.6	23.0
Ulna	Total length	—	58.0*
	Length of olecranon (to mid notch)	—	22.0
Lunar	Max. dorsoventral dimension	—	7.1
	Max. proximodistal dimension	—	4.1
	Max. mediolateral dimension	—	4.8
Scaphoid	Max. dorsoventral dimension	—	7.8
	Max. proximodistal dimension	—	3.2
	Max. mediolateral dimension	—	4.5
Pisiform	Max. dorsoventral dimension	—	7.3
Cuneiform	Max. dorsoventral dimension	—	5.4
	Max. proximodistal dimension	—	3.0
	Max. mediolateral dimension	—	4.4
Magnum	Max. dorsoventral dimension	—	6.2
	Max. proximodistal dimension	—	3.6
	Max. mediolateral dimension	—	4.0
Unciform	Max. dorsoventral dimension	—	3.7
	Max. proximodistal dimension	—	2.8
	Max. mediolateral dimension	—	3.0
Trapezium	Max. dorsoventral dimension	—	3.0
	Max. proximodistal dimension	—	2.5
	Max. mediolateral dimension	—	2.2
Mc I	Length	—	6.8
	Breadth (proximal, midshaft, distal)	—	3.2, 3.3, 3.5
Mc II	Length	—	—
	Breadth (proximal, midshaft, distal)	—	— , — , 5.2
Mc III	Length	—	11.5
	Breadth (proximal, midshaft, distal)	—	7.1, 5.6, 7.0
Mc IV	Length	—	8.2
	Breadth (proximal, midshaft, distal)	—	4.5, 3.4, 4.5
Manual Phalanx III-1	Length	—	4.2
	Breadth of proximal end	—	6.3
Manual Phalanx III-2	Length	—	4.5
	Breadth of proximal end	—	6.3
Manual Phalanx III-3	Length	—	13.0*
	Breadth of proximal end	—	6.3

*Approximate.

[1] From greater tuberosity to distal end.

curved. They are wider proximally and gradually taper towards the tip. One nearly complete distal phalanx has a narrow central fissure along its dorsal margin. As in *Alocodontulum*, this fissure is not particularly well developed, and it does not resemble the deep, broad fissures developed in terminal phalanges of pholidotans. There are small, but distinct, curving vascular grooves along the lateral surfaces of all distal phalanges.

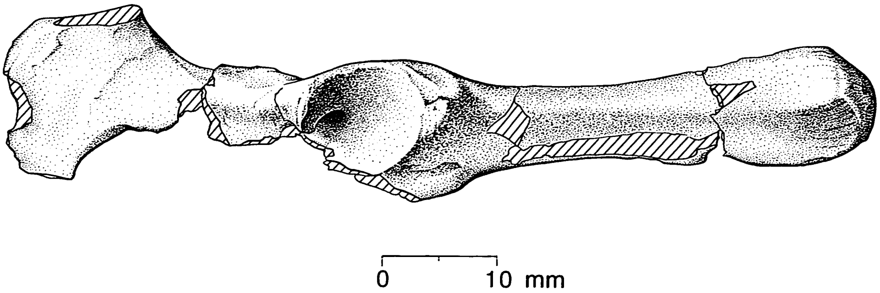

FIG. 13—***Brachianodon westorum*, UM 98743 (holotype), right pelvis in right lateral view.**

Measurements of forelimb elements of *Brachianodon westorum* are listed in Table 3.

HIND LIMB SKELETON

Pelvis—The right pelvis is relatively complete (Fig. 13), lacking only the pubis and some portions of the ischial margin. *Brachianodon* has a relatively long, narrow, outwardly curving ilium that terminates in a slightly elevated, rounded margin as in most other palaeanodonts. The ischial ramus is metacheiromyid-like in being in direct line with the ilium, not angled dorsally as in *Alocodontulum* and *Pentapassalus* (Rose et al., 1992). *Brachianodon* differs from all other known palaeanodonts in having a very short ischial ramus. The ischial ramus is broad mediolaterally as in *Palaeanodon*, but unlike that of *Metacheiromys* where the ramus is relatively narrow. The ischial blade is somewhat broken, but it appears to have been relatively broader than in other palaeanodonts. The ischial tuberosity extended dorsally well beyond the dorsal margin of the iliac blade.

Femur—The femur of *Brachianodon* (Fig. 14A,B) is similar to that of other palaeanodonts, but there are minor points of variation. The femoral head is rounded in *Brachianodon*, while is relatively more anteroposteriorly compressed in *Palaeanodon* and *Metacheiromys*. The greater trochanter does not project proximally beyond the head in *Brachianodon* but often does so in *Metacheiromys* and *Palaeanodon*. The femoral shaft is strongly flattened anteroposteriorly in *Brachianodon*, slightly less so in *Metacheiromys* and *Alocodontulum*, and it is more rounded in *Palaeanodon*. *Brachianodon* and *Metacheiromys* have a relatively wider patellar groove and an anteroposteriorly narrower distal end than does *Palaeanodon* or *Alocodontulum*. *Brachianodon* has a small third trochanter positioned slightly less than half way down the shaft. As in other metacheiromyids, the third trochanter is connected to the greater trochanter by narrow crest. This crest is very well developed in *Metacheiromys*, but is less robust in *Brachianodon* and *Palaeanodon*.

Patella—The patella of *Brachianodon* (Fig. 15) is slightly longer than it is wide, but has a generally rounded appearance. It is not markedly compressed anteroposteriorly.

Tibia—The tibia of *Brachianodon* is shown in Figure 14E,F. Morphologically, palaeanodont tibiae exhibit a great deal of variation. The tibial shaft can be bowed in both a sagittal and coronal plane as in *Brachianodon* and *Alocodontulum*, in a coronal plane alone as in some *Metacheiromys* specimens (e.g., UM 32782) and most *Palaeanodon* specimens, or in a sagittal plane alone as in other metacheiromyid specimens (e.g., UM 98811). In anterior view, the tibia of UM 98811 is bowed laterally at the proximal end and bowed medially at the distal end, producing a sigmoid tibial shaft.

Tibial condyles (plateaus) are at different heights in palaeanodonts, with the medial always lower (more distal) than the lateral. Continuous with the lateral tibial condyle in *Brachianodon* and posterior to it, is a small facet interpreted by Rose et al. (1992) to represent a popliteal

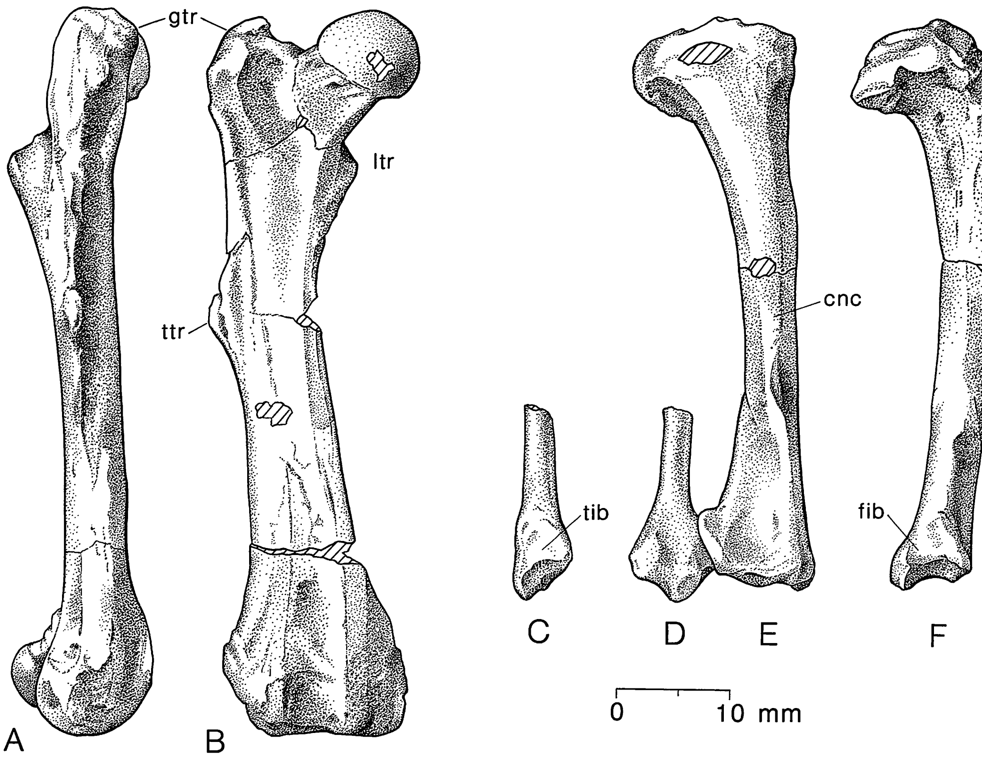

FIG. 14—*Brachianodon westorum*, UM 98743 (holotype), right hind limb. A-B, femur in lateral and anterior views. C-D, fibula in medial and anterior views. E-F, tibia in anterior and lateral views. Abbreviations: *cnc*, cnemial crest; *fib*, fibular facet; *gtr*, greater trochanter; *ltr*, lesser trochanter; *tib*, tibial facet; *ttr*, third trochanter.

sesamoid facet. This facet seems to be present in most palaeanodonts, but it appears to be variably developed in *Metacheiromys*. *Brachianodon*, like all metacheiromyids and primitive epoicotheriids (where known), lacks proximal fusion of the tibia and fibula.

Brachianodon has a fairly robust cnemial crest originating from the tibial tuberosity and extending nearly two-thirds of the way down the shaft (Fig. 14F). It terminates distally in a small elongated tubercle. *Palaeanodon* has a more robust cnemial crest that is more elevated anteriorly away from the shaft than in *Brachianodon*. This crest extends just below mid-shaft in *Palaeanodon*. *Metacheiromys* has a variably developed cnemial crest, ranging from one as robust as that of *Palaeanodon* to one that is almost non-existent. *Metacheiromys* typically has a very prominent cnemial tubercle positioned at mid-shaft. *Alocodontulum* has a cnemial crest similarly developed to that of *Brachianodon*, but it does not extend as far distally.

The distal tibia of *Brachianodon* is anteroposteriorly compressed and mediolaterally broad, with a very small medial malleolus. The fibular facet is elevated laterally away from the tibial shaft; it does not continue proximally up the shaft, and it is not sutural. The tibia of *Palaeanodon* is similar to that of *Brachianodon*, but it has a less anteroposteriorly compressed distal end and a more robust medial malleolus. *Palaeanodon* exhibits a variable tibia-fibula articulation, ranging from one like that of *Brachianodon*, to one that is proximally extended and sutural, to one that is solidly fused (Matthew, 1918; Simpson, 1931). It is not clear at this time if such differences have any taxonomic importance or whether they simply reflect onto-

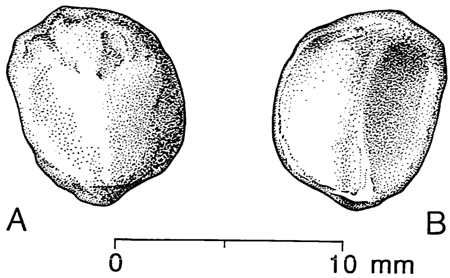

FIG. 15—*Brachianodon westorum*, UM 98743 (holotype), patella in anterior (A) and posterior (B) views.

genetic variation (Simpson, 1931). *Alocodontulum* is similar to *Brachianodon* in these features except that the fibular articular surface is not as elevated laterally.

Metacheiromys differs from *Brachianodon* and *Palaeanodon*, and from *Alocodontulum*, in combining a less anteroposteriorly-compressed distal tibia and a very weak medial malleolus. It exhibits variation similar to that of *Palaeanodon* in the distal tibia-fibula articulation, although it appears that the fibular articulation of the tibia always extends proximally up the shaft in *Metacheiromys* regardless of whether it is sutural or fused.

The length of the tibia relative to the femur (crural index) differs substantially among palaeanodonts (see Table 6). *Brachianodon* has a very short tibia compared to femur length, with a crural index of 78 or 78%. *Palaeanodon* has a crural index ranging from 84 to 92. The type specimen of *Metacheiromys tatusia* (AMNH 11549) has a relatively short tibia, with a crural index of 84, but other middle Eocene metacheiromyids have crural indices as high as 116.

Fibula—The fibula of *Brachianodon* is represented only by a right distal portion (Fig. 14C,D). A triangular tibial facet is located on the medial aspect just proximal to a small, semicircular astragalar facet. The distal tibial-fibular joint is not bipartite as in *Alocodontulum* (Rose et al., 1992). The lateral malleolus is not nearly as robust and does not project as far distally as it does in *Metacheiromys*. The fibular shaft becomes very narrow proximally, being much less robust than in *Metacheiromys* or *Alocodontulum*.

Tarsus—UM 98743 includes a complete right astragalus (Fig. 16H,I). The astragalus of *Brachianodon* differs from that in other palaeanodonts in being relatively much shorter. In medial view, the body is compressed proximodistally and is very deep dorsoplantarly. The astragalar neck is extremely short, so much so that the medial trochlear margin actually overlaps the dorsal surface of the neck. The neck is much shorter than in *Palaeanodon* or *Metacheiromys*, but it is approached by *Alocodontulum* in this condition. The medial trochlear ridge does not overlap the neck in *Alocodontulum*.

There is a deep groove on the dorsal surface of the astragalar neck for the anterior edge of the distal tibia during dorsiflexion. *Alocodontulum* has a shallow pit on the dorsal astragalar neck, while *Palaeanodon* and *Metacheiromys* lack either a pit or a groove.

The trochlear surface of the astragalus is shallowly grooved in *Brachianodon*. The trochlea is sharply rounded and compressed proximodistally compared with other palaeanodonts. In distal view, the astragalar head of *Brachianodon* is rounded, not dorsoplantarly compressed as in other palaeanodonts.

In plantar view, the astragalar head extends only slightly farther distally than the distal-most point of the lateral trochlear ridge. This emphasizes the "tucked-under" position of the astragalar head in *Brachianodon*, a condition not approached in any other known palaeanodont. Among living "edentates," the short "tucked-under" astragalar neck of *Brachianodon* is most closely approximated by that of *Manis*, but *Brachianodon* does not have the concave astragalar head (navicular facet) that pangolins have (Rose and Emry, 1993).

The sustentacular facet is separated from the navicular facet by a small ridge that forms the plantar border of the navicular facet in *Brachianodon*. The sustentacular facet is separated from the navicular facet by a relatively deep groove in *Palaeanodon*, *Metacheiromys*, and *Alocodontulum*, such that the two facets are not confluent. The calcaneal facet is oriented proximodistally in *Brachianodon*, *Palaeanodon*, and *Alocodontulum*, but it is oriented mediolaterally in *Metacheiromys*. The astragalar fossa is much deeper in *Brachianodon* compared to other palaeanodonts. Contrary to Matthew (1909), *Metacheiromys* often has a tiny astragalar foramen, but this feature has not been found in any other palaeanodont.

Calcaneal morphology in palaeanodonts is somewhat variable, but there are a number of shared characteristics. *Brachianodon*, as in all palaeanodonts, has a very short distal portion of the calcaneum (Fig. 16J). The distance from the distal aspect of the astragalar facet to the dorsal margin of the cuboid facet represents only about 20% of total calcaneal length. This is similar to the proportions found in *Metacheiromys*, while *Palaeanodon* has a slightly longer distal portion (approximately 25% of total calcaneal length).

Brachianodon has a well developed sustentacular facet positioned farther distally than in *Metacheiromys*, *Palaeanodon*, and *Alocodontulum*. The sustentacular facet is continuous with the proximomedial portion of the astragalar facet in *Brachianodon*; this facet is separated from the astragalar facet by a well developed groove in other palaeanodonts. Although the peroneal tubercle is broken, it clearly joined the dorsolateral margin of the cuboid facet as in other palaeanodonts. As in all other palaeanodonts, *Brachianodon* has a well developed distal plantar tubercle, but unlike other palaeanodonts, this tubercle projects distoplantarly beyond the distal surface of the cuboid facet. *Brachianodon* has a modest pit for a spring ligament medial to the cuboid facet; this is relatively smaller than in most other palaeanodonts.

The astragalar facet on the calcaneum is convex in *Brachianodon*, and it is oriented slightly oblique to the long axis of this bone. Among other palaeanodonts, *Brachianodon* most closely resembles *Palaeanodon* in astragalar facet morphology, except that in *Palaeanodon* this facet is much more steeply angled, such that the articular surface is oriented dorsoplantarly and faces almost directly mediad. *Metacheiromys* exhibits two different manifestations of the astragalar facet of the calcaneum. Some specimens of *Metacheiromys* are like *Palaeanodon*, while others have the astragalar facet facing directly distal, forming a transverse, vertical wall.

The calcaneal tuber is bowed dorsoplantarly in *Brachianodon*. The calcaneal tuber is relatively straight in all other palaeanodonts, except in some specimens of *Metacheiromys* that approach the condition present in *Brachianodon*. The proximal end of the *Brachianodon* calcaneum is not dorsoplantarly deep as in most other palaeanodonts, but instead is mediolaterally broad. There is a large tubercle developed on the medial aspect of the proximal end. A proximomedial tubercle is not present in any other palaeanodont, although *Alocodontulum* has a slight medial thickening in this area.

Pes—Portions of the left and right pes are included among skeletal elements represented by UM 98743. These include the left ectocuneiform and the second and fourth metatarsals, and the right ectocuneiform, mesocuneiform, and the second and third metatarsals.

The ectocuneiform (Fig. 16C-E) is deep dorsoplantarly, and it is slightly longer (proximodistally) than it is wide (mediolaterally). The proximal end is formed by the confluence of the navicular facet (angled distomedially) and the proximal cuboid facet (oriented proximodistally). These facets are distinguished proximally by a sharp angulation separating them. The distal end of the ectocuneiform is T-shaped and slightly concave dorsoplantarly.

The medial side of the ectocuneiform has dorsal and plantar facets for the second metatarsal along its distal margin. There is a dorsoplantarly elongate, rugose area separating these two facets from the distal margin of the navicular facet, representing the articular area for the mesocuneiform. On the lateral side, the ectocuneiform has two cuboid facets. The proximal cuboid facet is a relatively narrow, dorsoplantarly oriented, semilunate facet. The distal cuboid facet at the dorsal-most point of the lateral margin is tear-shaped and slightly convex.

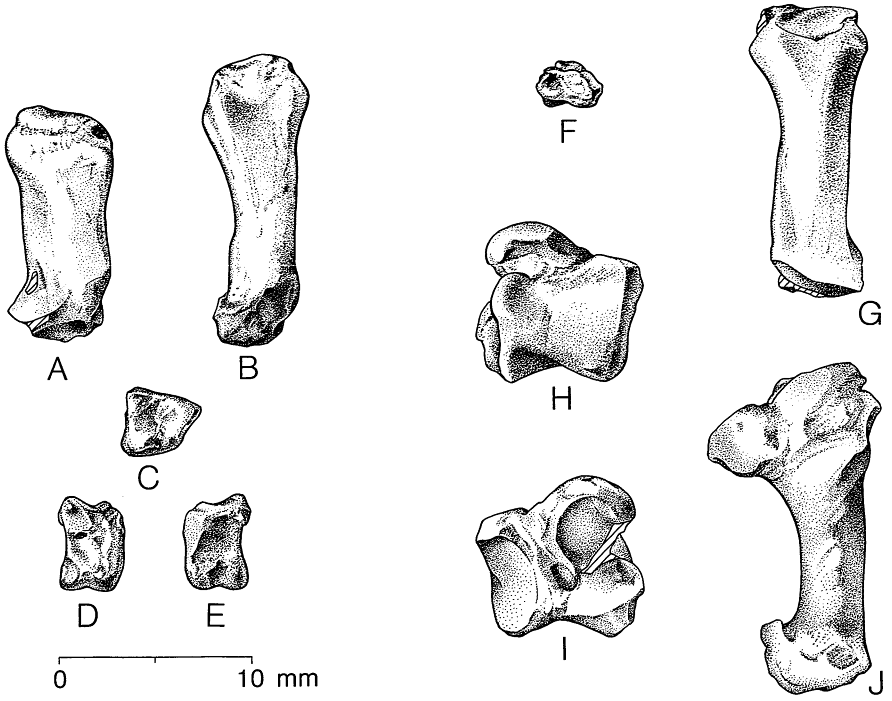

FIG. 16—*Brachianodon westorum*, UM 98743 (holotype), left and right tarsal elements and metatarsals. A, left metatarsal II in dorsal view. B, left metatarsal IV in dorsal view. C-E, left ectocuneiform in dorsal, lateral, and medial views. F, right mesocuneiform in dorsal view. G, right metatarsal III in dorsal view. H-I, right astragalus in dorsal and plantar views. J, right calcaneum in dorsal view.

The mesocuneiform is very compressed proximodistally (Fig. 16F). It is relatively broad mediolaterally, but very deep dorsoplantarly. Both the medial and lateral aspects lack distinct articular facets, but they do have rugose areas for ligamentous attachment to the entocuneiform and ectocuneiform, respectively. The proximal end is triangular with a shallow, concave facet for the navicular. The proximal end terminates in a small, pointed plantar process. The distal end of the mesocuneiform is also triangular, but the articular surface for the second metatarsal is flatter than the proximal articular surface.

Metatarsals of *Brachianodon* are, in general, less robust than the metacarpals. Mt II is shorter than Mt III or Mt IV, which are approximately the same length. All metatarsals have less robust shafts and less complex articular surfaces than do metacarpals.

The proximal end of the second metatarsal (Fig. 16A) is T-shaped with an essentially flat articular surface and a relatively well developed plantar tubercle. The medial side of the proximal end has two rugose areas for articulation with the first metatarsal. The dorsal rugosity is elongated proximodistally, while the plantar one is rounded. On the lateral side are dorsal and plantar facets for articulation with the ectocuneiform. The distal end of Mt II is asymmetric, with the medial side being deeper (dorsoplantarly) than the lateral side. The medial phalangeal facet is larger than the lateral one, and these facets are separated by a small ridge.

The proximal end of Mt III (Fig. 16G) is also T-shaped as in Mt II, but the dorsoplantar portion is not as wide, relatively, and the articular facet for the ectocuneiform is more convex

TABLE 4—Measurements of hind limb elements of *Brachianodon westorum*, UM 98743. Lengths of long bones are measured from proximal to distal articular surfaces. All measurements in mm.

		Left	Right
Pelvis	Ilium length	---	44.4
	Ischium length	---	31.2
Femur	Length (head to condyles)	---	63.6
	Distal end, transverse breadth	---	15.5
	Distal end, anteroposterior depth	---	11.3
Patella	Length	---	8.6
	Breadth	---	6.9
Tibia	Length	50.2	49.6
	Proximal transverse breadth	---	14.2
	Distal transverse breadth	10.9	11.6
Calcaneum	Length	---	16.7
Astragalus	Length	---	9.3
	Breadth of trochlea	---	7.5
Ectocuneiform	Max. dorsoventral dimension	5.1	---
	Max. proximodistal dimension	3.8	---
	Max. mediolateral dimension	3.8	---
Mesocuneiform	Max. dorsoventral dimension	---	4.7
	Max. proximodistal dimension	---	2.4
	Max. mediolateral dimension	---	3.5
Mt II	Length	12.3	---
Mt III	Length	---	15.3
Mt IV	Length	15.1	---

than flat. There is a distinct facet for the fourth metatarsal on the lateral side of the proximal end, but no distinct second metatarsal facets on the medial side. The distal end is symmetrical; it has medial and lateral phalangeal facets of equal size, separated by a more prominent ridge than on Mt II.

The proximal end of the fourth metatarsal (Fig. 16B) is strongly concave for articulation with the cuboid. The articular facet for the third metatarsal is continuous with the cuboid facet, but separated from it by a ridge or angulation. On the lateral side of the proximal end is a concave, proximodistally narrow, dorsoplantarly elongated, semilunate facet for articulation with the fifth metatarsal. The distal end is similar to that of Mt III, with phalangeal facets of equal size, but these are separated by a less robust ridge.

Other pedal phalanges and phalangeal fragments appear similar to those described for other palaeanodonts. Proximal and medial pedal phalanges are generally similar in shape to those of the manus, but not as robust.

Measurements of hind limb elements of *Brachianodon westorum* are listed in Table 4.

DISCUSSION

Some idea of the body size of *Brachianodon westorum* can be gained by comparing its long bone lengths and diameters to those of a range of generalized mammals (Table 5). Computed body mass estimates are conflicting and thus to some degree ambiguous (the maximum of all minimum estimated weights exceeds the minimum of all maximum estimated weights), but a weight in the range of 1 to about 2.7 kg appears reasonable. *Brachianodon westorum* was clearly larger than *Palaeanodon nievelti* and *Metacheiromys marshi* and smaller than *Palaeano-*

TABLE 5—Body size estimate for Eocene metacheiromyid *Brachianodon westorum* based on measurements of UM 98743. Diameters measured in parasagittal plane; metapodial measurements are those of the largest metacarpal and metatarsal (Mc III and Mt III). Predictions computed using program in Gingerich (1990).

Brachianodon westorum	Measurement (mm)	Predicted body mass (g)	95% Prediction limits Min (g)	Max (g)
Humerus length	51.1	1,029	305	3,476
Ulna length	58.0*	879	278	2,777
Metacarpal length	11.5	364	58	2,292
Femur length	63.6	1,086	297	3,968
Tibia length	49.6	312	84	1,159
Metatarsal length	15.3	186	28	1,237
Humerus diameter	7.6	3,125	1,724	5,662
Ulna diameter	6.6	—	—	—
Metacarpal diameter	4.8	11,185	4,581	27,308
Femur diameter	4.8	853	448	1,624
Tibia diameter	5.8	1,742	684	4,435
Metatarsal diameter	2.6	1,072	287	4,005
N, geom. mean, max., min.	11	**1,033**	4,581	1,159
Multiple regression All species:		11 L&D— **2,734**	6 L— 1,056	
(Artiodactyla removed):		(3,241)	(1,018)	

*Estimated

don ignavus and *Metacheiromys dasypus*; it was a little larger than *Alocodontulum atopum* (Rose et al., 1992).

We can draw some further inferences from Table 5. Each long bone measurement is used to generate an independent body mass estimate. All of these taken together yield the range from 1 to 2.7 kg. Individual estimates for humerus length, total ulna length, femur length, humerus diameter, femur diameter, tibia diameter, and metatarsal diameter lie within or close to this range. However, individual estimates for metacarpal length, tibia length, and metatarsal length fall far below the composite range (as would a functional measure of ulna length measured distal to the trochlear notch), while the individual estimate for metacarpal diameter falls far above it. Thus *Brachianodon* was a mammal with an unusually short ulna distal to the trochlear notch, unusually short tibia, unusually short metapodials, and an unusually robust largest metacarpal: all characteristics, taken together, that are consistent with interpretation as a fossorial mammal.

Simpson (1931, p. 316-319) noted that the digging motion of *Metacheiromys*, like that of modern fossorial "edentates," involved movement of the hands toward the midline of the body, with earth being pushed back beneath it. The robust metacarpals and proximal phalanges of *Brachianodon*, differing ranges of motion permitted between these, and evidence of a strong dorsal ligament binding Mc III to more distal phalanges (especially III-3) give some indication of how the manus functioned during digging. Digging evidently involved forcing a compact extended manus forward into the soil in front of the animal, with metacarpals and phalanges aligned, and nearly straight terminal phalanges fully extended, all stabilized by strong dorsal and plantar ligaments. When the manus as a whole was flexed and retracted to move soil backward beneath the body, the claw-bearing terminal phalanges were also flexed to aid in this.

TABLE 6—Comparison of femur length and tibia length in *Brachianodon westorum* to those of other Eocene palaeanodonts. All measurements in mm.

	Femur length	Tibia length	Crural index (%)
Middle Eocene			
Cf. *Metacheiromys* sp. (UM 98811; undescribed)	62.6	72.4	116
Metacheiromys dasypus (UM 32782; undescribed)	82.3	83.5	101
Metacheiromys tatusia (AMNH 11549; Simpson, 1931, p. 353)	49.4	41.6	84
Brachianodon westorum (UM 98743; this paper)	63.6	49.6	78
Early Eocene			
Palaeanodon sp. (UM 71530; undescribed)	72.8	66.8	92
Alocodontulum atopum (UM 93740; Rose et al., 1992, p. 242)	60.3	51.9	86
Palaeanodon ignavus (AMNH 15137; Matthew, 1918, p. 639)	80.0	67.5	84

Brachianodon is unusual among palaeanodonts in having a short distal hind limb segment, as indicated by its short tibia relative to femur length (Table 6). This may mean that it was a more powerful digger than either *Palaeanodon* or *Metacheiromys*, but definitive interpretation will require more complete remains of all of these taxa.

The presence of *Brachianodon* in the early Bridgerian indicates that at least two very distinct lineages of metacheiromyids were present in the middle Eocene. *Brachianodon* is intermediate between *Palaeanodon* and *Metacheiromys* in a number of features, but it is anatomically unique in others. *Brachianodon* and *Metacheiromys* were probably derived from *Palaeanodon* or a *Palaeanodon*-like common ancestor. With *Brachianodon* removed from the *Metacheiromys* complex, specimens referred to *Metacheiromys* are still highly variable, which suggests that metacheiromyid palaeanodonts were much more diverse in the middle Eocene than previously recognized.

Comparison of hind limb proportions of middle Eocene metacheiromyids in Table 6 shows how these differ from each other. Four middle Eocene specimens, two published and two new, are complete enough to permit calculation of a crural index, and all four have very different indices. Hind limb proportions of *Brachianodon westorum* described here (crural index of 78 or 78%) are closest to those of *Metacheiromys tatusia* described by Simpson (1931; crural index of 84), but these differ sufficiently in size, dental formula, and other characteristics to warrant separation in different genera. *Metacheiromys dasypus*, as represented by UM 32782, has a crural index of 101%, while another new *Metacheiromys*-like specimen, UM 98811, has a tibia much longer than the femur (and a crural index of 116%), long metatarsals, and evidently long phalanges.

It is not clear from the published literature that *M. tatusia* and *M. dasypus* belong in the same genus, nor that they represent *Metacheiromys*. There is probably at least one new genus of metacheiromyid in the middle Eocene in addition to *Metacheiromys* and *Brachianodon*, but sorting out which specimens with two postcanine teeth are really *Metacheiromys* and which represent a different genus will require a better skeleton of the type species *M. marshi*. If Schoch (1984) is correct in synonymizing *M. tatusia* with *M. marshi*, then the required skeleton preserving limb proportions is known. However, Simpson (1931, p. 306) believed it probable that *M. marshi* and *M. tatusia* are distinct.

Ordinal relationships of palaeanodonts are unclear. Matthew (1918) described palaeanodonts as a suborder of Edentata, but recognized that their affinities might lie with pholidotans (pangolins) or xenarthrans (sloths, anteaters, and armadillos), or both. Emry (1970) argued for a palaeanodont-pholidotan relationship (also see Rose and Emry, 1983, 1993; Rose et al., 1992), while Rose (1978, 1979) suggested that pholidotans, xenarthrans, and palaeanodonts may form a monophyletic clade, a position supported by Schoch (1984). Recently, Patterson et al. (1992) argued that palaeanodonts and xenarthrans may share common ancestry, a position suggested too by Simpson (1931). Whatever the ordinal relationships of palaeanodonts, it is almost certain that epoicotheriids and metacheiromyids share a common ancestry and form a monophyletic group (Rose et al., 1991).

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LITERATURE CITED

COLBERT, E. H. 1942. An edentate from the Oligocene of Wyoming. Notulae Naturae, 109: 1-16.

DOUGLASS, E. 1905. The Tertiary of Montana. Memoirs of the Carnegie Museum, 2: 203-224.

EMRY, R. J. 1970. A North American Oligocene pangolin and other additions to the Pholidota. Bulletin of the American Museum of Natural History, 142: 455-510.

FLOWER, W. H. 1885. An introduction to the osteology of the Mammalia. Third Edition. London: Macmillan and Company, 382 pages.

GALTON, J. C. 1870. The muscles of the fore and hind limbs in *Dasypus sexcinctus*. Transactions of the Linnean Society, London, 26: 523-565.

GAZIN, C. L. 1952. The lower Eocene Knight Formation of western Wyoming and its mammalian faunas. Smithsonian Miscellaneous Collections, 117: 1-82.

GINGERICH, P. D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. University of Michigan Papers on Paleontology, 28: 1-97.

———. 1990. Prediction of body mass in mammalian species from long bone lengths and diameters. Contributions from the Museum of Paleontology, University of Michigan, 28: 79-92.

GUTHRIE, D. A. 1967. The mammalian fauna of the Lysite Member, Wind River Formation, (early Eocene) of Wyoming. Memoirs of the Southern California Academy of Sciences, 5: 1-53.

MATTHEW, W. D. 1906. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Memoirs of the American Museum of Natural History, 9: 291-567.

———. 1918. A revision of the lower Eocene Wasatch and Wind River faunas. Part V. Insectivora (continued), Glires, Edentata. Bulletin of the American Museum of Natural History, 38: 565-657.

PATTERSON, B., W. SEGALL, W. D. TURNBULL, and T. J. GAUDIN. 1992. The ear region in xenarthrans (=Edentata: Mammalia). Part II. Pilosa (sloths, anteaters), palaeanodonts, and a miscellany. Fieldiana Geology, New Series, 24: 1-79.

ROSE, K. D. 1978. A new Paleocene epoicotheriid (Mammalia), with comments on the Palaeanodonta. Journal of Paleontology, 52: 658-674.

———. 1979. A new Paleocene palaeanodont and the origin of the Metacheiromyidae (Mammalia). Breviora, 455: 1-14.

———. 1990. Postcranial skeletal remains and adaptations in early Eocene mammals from the Willwood Formation, Bighorn Basin, Wyoming. Geological Society of America Special Paper, 243: 107-133.

——— and R. J. EMRY. 1983. Extraordinary fossorial adaptations in the Oligocene palaeanodonts *Epoicotherium* and *Xenocranium* (Mammalia). Journal of Morphology, 175: 33-56.

——— and ———. 1993. Relationships of Xenarthra, Pholidota, and fossil "edentates": the morphological evidence. In F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny, Springer-Verlag, New York, pp. 81-102.

———, ———, and P. D. GINGERICH. 1992. Skeleton of *Alocodontulum atopum*, an early Eocene epoicotheriid (Mammalia, Palaeanodonta) from the Bighorn Basin, Wyoming. Contributions from the Museum of Paleontology, University of Michigan, 28: 221-245.

———, L. KRISHTALKA, and R. K. STUCKY. 1991. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 11. Palaeanodonta (Mammalia). Annals of the Carnegie Museum, 60: 63-82.

SCHOCH, R. M. 1984. Revision of *Metacheiromys* Wortman, 1903 and a review of the Palaeanodonta. Postilla, 192: 1-28.

SIMPSON, G. G. 1931. *Metacheiromys* and the Edentata. Bulletin of the American Museum of Natural History, 59: 295-381.

WINDLE, B. C. A. and F. G. PARSONS. 1899. On the myology of the Edentata. Part I. Muscles of the head, neck, and fore limb. Proceedings of the Zoological Society of London, 1899: 314-339.