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**Revision of
Metacheiromys Wortman, 1903
And a Review of the Palaeanodonta**

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(Received 21 April 1983)

Abstract

Two species of the middle Eocene palae-anodont (Mammalia) genus *Metacheiromys*, *M. marshi* Wortman, 1903 (= *M. tatusia* Osborn, 1904) and *M. dasyplus* Osborn, 1904 (= *M. osborni* Simpson, 1931), are recognized as valid. The previously described Palaeanodonta (Edentata) are reviewed and a new subfamily, Propalaeandontinae, is erected for *Propalaeandon*. *Propalaeandon* is the plesiomorphous sister-group of the remaining metacheiromyids. The Epocoicotheriidae is a paraphyletic family including the monophyletic Epicoicotheriinae and a number of poorly known genera that can not presently be assigned to distinct subfamilies.

Key Words

Metacheiromys, Palaeandonta, Edentata, Propalaeandontinae, indeterminate Primates, fossil mammals.

Introduction

The Palaeandonta are an extinct, archaic group of Paleocene to Oligocene, edentatelike mammals of uncertain affinities

which, with one exception, are known solely from the early Tertiary of the Rocky Mountain region of the western United States. The one possible exception is a palaeandont specimen reported from the Oligocene of West Germany (Heissig, 1982). *Metacheiromys* Wortman, 1903, was the first genus of palaeandonts to be described; however, this genus has never been photographically illustrated and has not been critically reviewed since Simpson's (1931) classic study. In the past decade there has been a resurgence of interest in the Palaeandonta and a number of new species have been described (West, 1973; Rose, Bown and Simons, 1977; Rose, 1978, 1979; Heissig, 1982; Rose and Emry, 1983). However, no systematic review of the known genera and species of palaeandonts has been attempted. Here I revise the species-level taxonomy of *Metacheiromys* and illustrate the genoholotype and the more important referred specimens housed in the Peabody Museum of Natural History (including specimens which have been newly discovered in the Peabody Museum Collections). Finally, I briefly review the known Palaeandonta.

Abbreviations

Institutions
AMNH American Museum of Natural History, New York City
YPM Vertebrate Paleontology Collections, Peabody Museum of Natural History, Yale University, New Haven

YPM O Osteology Collections, Peabody
Museum of Natural History,
Yale University, New Haven

Statistics

CV Coefficient of Variation

M Mean

OR Observed range

SD Standard deviation

All measurements were taken with a Helios
dial caliper and are expressed in millimeters.

Systematic Paleontology

CLASS Mammalia Linnaeus, 1758, p. 14
SUBCLASS Theria Parker & Haswell, 1897,
p. 448
INFRACLASS Tribosphenida McKenna, 1975,
p. 25
SUPERCORHORT Eutheria Gill, 1872, p. 1
COHORT Edentata Cuvier, 1798, p. 142
ORDER Palaeanodonta Matthew, 1918, p. 620

Discussion

The two families Metacheiromyidae Wortman (1903, p. 347) and Epoicotheriidae Simpson (1927, p. 285) have generally been regarded as closely related and have been placed together in Matthew's (1918) suborder Palaeanodonta (Colbert, 1942; Simpson, 1945, 1959; Rose, 1978, 1979; but for a contrary view, see Emry, 1970). As Rose (1978, p. 665) has recently noted, the Palaeanodonta are recognizable by the following suite of characters:

- 1) Distinctive, large canines which show normal occlusion; i.e., the lower canines occlude in front of the upper canines (Colbert, 1942).
- 2) The progressive reduction in size and number of cheek teeth.
- 3) The progressive reduction and loss of enamel on the cheek teeth.
- 4) Development of a posteriorly-placed medial buttress on the mandible with an internal mandibular groove beneath it.
- 5) A fossorially adapted skeleton.

Matthew (1918) originally proposed the Palaeanodonta as a suborder of the order

Edentata, but also suggested that it might show affinities with both the Pholidota (pangolins) and Xenarthra (Edentata). Subsequently, most authorities (e.g., Simpson, 1931, 1945; Colbert, 1942; Gazin, 1952) placed the Palaeanodonta in the Edentata; Simpson (1931) argued strongly against pholidotean ties for the Palaeanodonta. In 1970, Emry described a new manid, *Patriomanis*, and discussed the then known palaeanodonts and pangolins. He concluded that the manids were derived from the metacheiromyids and thus placed the palaeanodonts in the order Pholidota. However, Emry dropped the use of the term Palaeanodonta "since the mutual affinities of the three families are not clearly known" (Emry, 1970, p. 507). Rose (1978, 1979) has recently suggested, on the basis of new material, that the Xenarthra, Pholidota and Palaeanodonta together form a monophyletic clade relative to other eutherians, but the relationships within this trichotomy (i.e., which two groups are more closely related to each other relative to the third) is as yet unresolved. Szalay (1977) came to essentially the same conclusions on the basis of a reconsideration of the astragalocalcaneal complex of these three groups. Here I adopt Szalay's (1977) higher level classification of the Palaeanodonta and tentatively consider this group to be a distinct order which is possibly referable, along with the orders Xenarthra Cope (1889, p. 657) and Pholidota Weber (1904, p. 412), to the cohort Edentata Cuvier (1798, p. 142).

FAMILY Metacheiromyidae Wortman, 1903, p. 347

SUBFAMILY Metacheiromyinae Wortman, 1903, p. 347

Metacheiromys Wortman, 1903, p. 347

Type Species

Metacheiromys marshi Wortman, 1903
(=*M. tatusia* Osborn, 1904).

Included Species

The type species and *M. dasypus* Osborn, 1904 (= *M. osborni* Simpson, 1931).

Distribution

Middle Eocene (Bridgerian) of the Bridger Formation, Bridger Basin, Wyoming.

Revised Diagnosis

Metacheiromyines distinguished by the following features: dental formula $\frac{0.1.1}{1.1.2}$; canines large, compressed (with triangular bases) and enamel-bearing; postcanines small (vestigial), single-rooted; most of length of jaw edentulous; shelf for lower horny plate not grooved, narrower and less conspicuous than in *Palaeanodon*; and ossified bullae complete.

***Metacheiromys marshi* Wortman, 1903, p. 347**

(Figs. 1–5; 7A, C; 8; 9)

Synonymy

Metacheiromys marshi Wortman, 1903, p. 347, figs. 105–108 (non fig. 109)

Metacheiromys tatusia Osborn, 1904, p. 165

Metacheiromys marshi: Simpson, 1931, p. 303, figs. 3A, 13A, 19

Metacheiromys tatusia: Simpson, 1931, p. 305, figs. 1, 3B, 13B–F, 15A, 18, 20, 21 (non fig. 22)

Metacheiromys tatusia: Emry, 1970, fig. 30C

Metacheiromys sp.: Szalay, 1977, fig. 12B

Lectotype

YPM 12903, left dentary with root of canine and alveoli for first two postcanines (Fig. 1A–C). Lectotype selected from the original type material by Simpson (1931, p. 304).

Paralectotypes

YPM 12903 (the following specimens may pertain to the same individual as that represented by the lectotype), right maxilla fragment bearing a broken canine (Fig. 1E, F); left upper canine (Fig. 1G, H); glenoid cavity of right scapula (Fig. 1K–M); proximal and distal ends of right humerus (Fig. 2); proximal two-thirds of right ulna (Fig. 3A–C); axis of second cervical vertebra which is missing the odontoid process (Fig. 1I, J); skull fragments; vertebral fragments (mostly cervical, thoracic and caudal centra); rib fragments; and distal end of radius.

Original syntypes subsequently excluded from the genus and referred to the order Primates, genus indeterminate (Simpson, 1931, p. 304): YPM 12903, right acetabular part of pelvis (Fig. 7B); proximal and distal ends of right tibia (Fig. 6).

Horizon and Locality of YPM 12903

Middle Eocene, probably Bridger B at Grizzly Buttes, Bridger Formation, Bridger Basin, Wyoming.

Discussion of YPM 12903

As Osborn (1904) and Simpson (1931) noted, all of the specimens catalogued under YPM 12903 were presumably collected together (although the collector and date are unknown, presumably collected by a Yale Scientific Expedition in the early 1870s), but represent parts of at least two individuals without duplication of any parts. Thus, YPM 12903 includes parts of the skull, dentary, forelimb and vertebral column of a metacheiromyid and parts of the pelvis and hindlimb of a primate.

Holotype of *Metacheiromys tatusia*

AMNH 11549, skull, right dentary and the majority of the skeleton (described and illustrated by Simpson, 1931).

Horizon and Locality of AMNH 11549

Collected in 1903 by Albert Thomson from middle Eocene-aged strata, Bridger B₂ at Grizzly Buttes, Bridger Formation, Bridger Basin, Wyoming.

Specimens Referred to *M. marshi* in the Peabody Museum

YPM 13500, proximal end of right humerus; fragments of distal ends of right and left humeri; proximal and distal ends of both femora (Fig. 4B, C, G); proximal ends of both tibiae; and miscellaneous vertebrae: collected by J. W. Chew in 1873 from middle Eocene-aged strata, probably Bridger C, at Dry Creek, Bridger Formation, Bridger Basin, Wyoming.

YPM 13501, fragments of pelvis, including parts of right and left ischia (Fig. 9); fragments of left femur; proximal and distal ends of right and left tibiae (Fig. 5); proximal half of right fibula (still in matrix); partial articulated tarsus and metatarsus (Fig. 8A, B) of right pes; miscellaneous phalanges and sesamoids, including an ungual phalanx of the ?manus (Fig. 8D–F); poorly-preserved vertebral centra of the thoracic and lumbar series; and first seven caudal vertebrae preserved articulated and partly embedded in matrix (Fig. 9). According to Simpson (1931, p. 305), YPM 13501 originally included the last two sacrals. Traces of glue and a fresh break are evident on the anterior surface of the first preserved caudal of YPM 13501, but the two sacrals mentioned by Simpson (1931) have presumably been lost since he described this specimen. YPM 13501 was collected by the Yale Scientific Expedition of 1873 from middle Eocene-aged strata, probably Bridger B, but possibly Bridger C, at Grizzly Buttes, Bridger Formation, Bridger Basin, Wyoming.

YPM 13502, posterior left dentary fragment with base of ascending ramus (Fig. 1D); miscellaneous vertebral centra including an axis missing the odontoid process and a number of caudals; glenoid cavity of right scapula; proximal ends of both humeri; distal

end of right humerus; a nearly complete sacrum with partial left ilium and acetabular part of pelvis (Fig. 8C); proximal end of right femur; distal ends of right and left femora (Fig. 4A, D, H); proximal ends of right and left tibiae; distal end of right tibia; and miscellaneous isolated foot bones, including an ungual phalanx: collected by the Yale Scientific Expedition of 1873 from middle Eocene-aged strata, Bridger B at Grizzly Buttes, Bridger Formation, Bridger Basin, Wyoming.

YPM 13503, broken vertebral centra, including axis of second cervical vertebra missing the odontoid process; proximal end of right humerus; distal fragments of right and left humeri; proximal end of right femur; distal end of left femur; proximal end of left tibia; right ilium and acetabular part of pelvis (Fig. 7A); proximal end of left ilium and acetabular part of pelvis; and incomplete sacrum (Fig. 7C): locality data the same as for YPM 13502.

YPM 40066, proximal end of right femur; distal end of right femur; proximal end of right humerus: no locality data; this specimen bears YPM Accession number 1072 which indicates that it was in O. C. Marsh's possession in 1877; presumably from the Bridger Basin, Wyoming.

YPM 40067, miscellaneous vertebral centra and rib fragments; glenoid cavities of both scapulae; partial left humerus; part of shaft of right humerus; left ulna (Fig. 3D, E); proximal half of left radius (Fig. 4E, F); miscellaneous foot bones and bone fragments: collected by J. F. Page from middle Eocene-aged (Bridgerian) strata of the Bridger Formation in the area of Grizzly Buttes, Bridger Basin, Wyoming, 6 September 1871.

Revised Diagnosis

Smallest known species of *Metacheiromys*; two lower postcanines approximately subequal in size.

Metacheiromys dasypus* Osborn, 1904,*p. 164**

(Fig. 10)

Synonymy*Metacheiromys dasypus* Osborn, 1904, p. 164*Metacheiromys dasypus*: Simpson, 1931, p. 306, figs. 3C, 4–8, 10–12, 14, 15B, 15C, 16, 17, 22*Metacheiromys osborni* Simpson, 1931, p. 306, fig. 3D*Metacheiromys dasypus*: Emry, 1970, fig. 28C**Holotype**

AMNH 11718, skull, jaws and partial skeleton.

Horizon and Locality of the TypeCollected by Walter Granger in 1903 from middle Eocene-aged strata, Bridger B₂ at Grizzly Buttes, Bridger Formation, Bridger Basin, Wyoming.**Holotype of *Metacheiromys osborni***

AMNH 12119, right dentary and anterior part of left dentary.

Horizon and Locality of AMNH 12119Collected by P. Miller in 1904 from middle Eocene-aged strata, Bridger D₂ at Lone Tree, Bridger Formation, Bridger Basin, Wyoming.**Referred Specimens**

YPM 40068, proximal end of left humerus; proximal end of left femur; proximal end of right tibia; partial right astragalus (Fig. 10A, C); right cuboid (Fig. 10B, D); miscellaneous phalanges, other foot bones and bone fragments: collected by G. G. Lobdell from middle Eocene-aged (Bridgerian) strata, Bridger Formation, in the Grizzly Buttes area, Bridger Basin, Wyoming, 4 September 1871.

YPM 40069 (YPM Accession number 511), head of right astragalus; two incomplete metatarsals; first phalanx of second digit of left pes (Fig. 10E, F); first and second phalanges of second digit of right pes: collected by S. Smith and J. W. Chew on 17 September 1873 from middle Eocene-aged strata, probably Bridger B, Bridger Formation, Bridger Basin, Wyoming.

Revised DiagnosisLargest known species of *Metacheiromys*, approximately 75% larger than *M. marshi*; second lower postcanine much smaller than first.**Description of *Metacheiromys***The known morphology of *Metacheiromys* is adequately described in Wortman (1903) and Simpson (1931). However, these works are illustrated only by simple line drawings. Therefore, I supplement Wortman's and Simpson's descriptions by photographically illustrating the genoholotype and selected referred specimens of *Metacheiromys* (Figs. 1–10). Except for differences in absolute size and relative size of the second lower postcanines, the two species are identical in known morphology.**Discussion of *Metacheiromys***In 1903, as part of a study of the Eocene mammals in the Marsh Collection of the Yale Peabody Museum, Jacob L. Wortman described a new genus and species of "primate," *Metacheiromys marshi*, based upon YPM 12903. Primate affinities for *Metacheiromys* were based primarily on the tibia (Fig. 6) which is distinctly primate in morphology (see discussion by Wortman, 1903, p. 351). He allied his new taxon with the extant aye-aye of Madagascar, *Daubentonia* (= *Cheiromys*). Wortman was under the impression that the materials catalogued under YPM 12903 pertained to a

single individual. However, as noted above, YPM 12903 is a composite of at least two individuals of approximately the same size and without duplication of any elements: parts of the head, forequarters and vertebral column of a palaeonodont and parts of the hindquarters of a primate. Thus, he was misled as to the affinities of *Metacheiromys*.

Also in 1903, an American Museum of Natural History field party led by Walter Granger discovered two partial "edentate" skeletons in the Eocene Bridger Formation of Wyoming, AMNH 11549 and AMNH 11718 (Simpson, 1931). Upon study, it was quickly recognized that these skeletons pertained to Wortman's genus, that *Metacheiromys* was an "edentate" and that YPM 12903 was a composite specimen. Osborn (1904) published a brief (three unillustrated pages) announcement clarifying the status of *Metacheiromys marshi* and coined the names *Metacheiromys tatusia* and *M. dasypus* for AMNH 11549 and AMNH 11718 respectively. In 1918 Matthew described in detail the closely related genus *Palaeonodon* and discussed the relationships of the *Metacheiromyidae*. However, it was left to Simpson (1931) to describe, illustrate and discuss the genus *Metacheiromys*.

Osborn (1904) distinguished *M. dasypus* as being much larger than *M. marshi*, and *M. tatusia* as being smaller than *M. marshi*. As Simpson (1931) noted, *M. dasypus* is considerably larger (by about 75%) than *M. marshi/tatusia* and is also distinguished by a relative reduction in size of the second lower cheek tooth. Simpson (1931) also noted that the lectotype of *M. marshi* is only slightly larger and heavier (more rugose) than the holotype of *M. tatusia*. Indeed, Simpson (1931, pp. 305–6) stated that "it is quite possible that a large series of specimens would show *M. tatusia* and *M. marshi* to intergrade completely." However, Simpson (1931) retained these species as distinct. Furthermore, Simpson described a fourth species of *Metacheiromys*, *M. osborni*, on the basis of a single dentary, AMNH 12119, that is "slightly longer than in *M. dasypus* (about 10%), stouter, canine larger, bone

more swollen around alveolus" (Simpson, 1931, p. 306).

I believe that the specific distinctions between *M. marshi* and *M. tatusia*, and between *M. dasypus* and *M. osborni* are extremely dubious. Rose (1978) has suggested that palaeonodonts may have been sexually dimorphic, as is the extant edentate anteater *Myrmecophaga* (Grassé, 1955). However, even without the presence of pronounced sexual dimorphism, the differences seen between the presumed species within each pair (*M. marshi/tatusia* and *M. dasypus/osborni*) are extremely slight and suggest that they may be due to individual variation (confounded in part by differing ontogenetic ages of the individuals concerned). In analogy, within the single species of the extant cingulate (Edentata), *Dasyopus novemcinctus* (the nine-banded armadillo), as represented by osteological specimens in the Peabody Museum of Natural History, I found as much variation in size and robustness among individuals as is seen between *M. marshi-M. tatusia* and *M. dasypus-M. osborni* (Tables 1 and 2). Furthermore, I have found Simpson's (1931) allocations of small specimens of *Metacheiromys* to either *M. tatusia* or *M. marshi* to be unreplicable. YPM 13501, a specimen which Simpson referred to the smaller *M. tatusia* includes some limb bones which, if anything, are slightly larger than some which he referred to *M. marshi*. Simpson referred only three specimens to *M. dasypus/osborni*, two of which are the holotypes. The third specimen, a few fragments of a hind foot of *Metacheiromys* (YPM 40069: Fig. 10E, F), shares no elements in common with the two type specimens.

Taking all of the above considerations into account, I recognize only two species of *Metacheiromys*, *M. marshi* Wortman, 1903 (= the junior subjective synonym *M. tatusia* Osborn, 1904) and *M. dasypus* Osborn, 1904 (= the junior subjective synonym *M. osborni* Simpson, 1931).

With this synonymy in mind, the biostratigraphic distribution of *Metacheiromys* can be reviewed (cf. Simpson, 1931, p. 307).

Table 1Metric data on *Dasypus novemcinctus*.

YPM O Number	Length upper cheek tooth row		Length lower cheek tooth row		Depth of mandible between 4th & 5th cheek teeth	
	Right Side	Left Side	Right Side	Left Side	Right	Left
2333	23.7	23.7	25.5	24.5	5.4	5.4
2334	25.1	25.0	26.2	26.0	5.6	5.5
2739	23.7	23.5	23.2	23.7	5.1	5.2
2740	26.5	26.4	28.1	27.3	6.8	6.8
4474	26.1	25.8	26.4	27.1	6.2	7.2
9505	22.5	22.8	22.6	22.9	5.3	5.0
10065	24.7	24.3	26.2	25.8	6.3	6.2
OR	22.5–26.5	22.8–26.4	22.6–28.1	22.9–27.3	5.1–6.8	5.0–7.2
M	24.61	24.50	25.46	27.70	5.81	5.90
SD	1.42	1.30	1.93	1.75	0.63	0.85
CV	5.77	5.31	7.58	6.32	10.84	14.41
Lowest observed value as a % of highest observed value	84.9	86.4	80.4	83.9	75.0	69.4

Table 2Metric data on *Metacheiromys*.

	Depth of dentary at mental foramen	Length of lower cheek tooth row
<i>M. marshi</i> , type	6.1	3.9
<i>M. tatusia</i> , type	5.0	3.8
Lower value as a % of higher value	82.0	97.4
<i>M. dasypus</i> , type	8.1	6.4
<i>M. osborni</i> , type	9.7	5.9
Lower value as a % of higher value	83.5	92.2

In the Bridger Basin, Wyoming, both *M. marshi* and *M. dasyopus* are known from as low as the Bridger B₂ (Matthew, 1909). The highest known stratigraphic occurrence of *M. marshi* is probably in the Bridger C, whereas *M. dasyopus* is known as high as the Bridger D₂ level.

A Review of the Known Palaeanodonta

In this section I review the published record of palaeanodonts and briefly discuss the salient characters of each genus.

ORDER Palaeanodonta Matthew, 1918, p. 620

FAMILY Metacheiromyidae Wortman, 1903, p. 347

Included Genera

Propalaeanodon, *Palaeanodon* and *Metacheiromys*.

Discussion

The Metacheiromyidae appear to be a distinct clade within the Palaeanodonta. [Character-state polarities can be assessed for palaeanodonts by making the reasonable assumption that *Amelotabes* (see below) is generally the most primitive known palaeanodont (Rose, 1978).] Early in the course of their evolution, the metacheiromyids reduced the postcanine teeth to small, cylindrical pegs, with blunt, rounded crowns that lacked enamel, and were separated by short diastemata. These character-states were converged upon by derived epicootheriids. The metacheiromyids retained the symplesiomorphy of a relatively long dentary [which may have been covered by a horny plate (derived)] and they are united by the synapomorphic feature of lacking occlusion between the postcanines and thus they do not show occlusal wear on these teeth as do the epicootheriids (Rose, 1979).

SUBFAMILY Propalaeanodontinae, new

Sole Included Genus

Propalaeanodon.

Diagnosis

Metacheiromyids with seven lower postcanines.

Discussion

The Metacheiromyinae, *Palaeanodon* and *Metacheiromys*, are united (relative to *Propalaeanodon*) by the further reduction in size and number of the postcanines and form a tight clade. *Propalaeanodon* is the plesiomorphous sister taxon of *Palaeanodon* and *Metacheiromys* and thus is here placed in the subfamily Propalaeanodontinae, of equal rank with the Metacheiromyinae.

Propalaeanodon Rose, 1979, p. 2

Type Species

Propalaeanodon schaffi Rose, 1979, p. 3.

Included Species

Only the type species.

Distribution

Late Paleocene (late Tiffanian) of the Bighorn Basin, Wyoming.

Discussion

Propalaeanodon, the oldest and most primitive metacheiromyid, is distinguished by the possession of seven lower postcanines which are all single-rooted except for the fourth which is double-rooted. The crowns of the postcanines are higher and more pointed than in *Palaeanodon* and the posterior medial buttress of the mandible is prominent, but less so than in *Palaeanodon*.

Propalaeanodon is known only from the holotype dentary and possibly two left humeri which Rose (1979) tentatively referred to this genus. Except for differences in size, these humeri are similar morphologically to the humeri of *Palaeanodon* and *Pentapassalus* (Rose, 1979).

SUBFAMILY Metacheiromyinae Wortman, 1903, p. 347, new rank

Included Genera

Palaeanodon and *Metacheiromys*.

Discussion

The metacheiromyines are united by the further reduction in size and number of the postcanines (five in the dentary of *Palaeanodon* and two in the dentary of *Metacheiromys*) relative to *Propalaeanodon*.

Note on Authorship of the Subfamily

Under the present rules of the International Code of Zoological Nomenclature (Stoll et al., 1964), the first author of any family-group taxon (e.g., tribe, subfamily, family, superfamily) is credited with authorship of all coordinate family-group taxa. Previously it was customary (and this is still often done) to credit authorship of a name to "he who first published it with exactly the spelling adopted in a given case" (Simpson, 1945, p. 31; cf. Van Valen, 1966, p. 109). I find the present rules "frequently unjust and confusing" (Simpson, 1945, p. 31) and would prefer the use of Simpson's (1945) criterion of authorship cited above.

***Palaeanodon* Matthew, 1918, p. 621**

Type Species

Palaeanodon ignavus Matthew, 1918, p. 622.

Included Species

The type species, *P. parvulus* Matthew, 1918, p. 640 and *Palaeanodon* sp. (Rose, 1978, 1979, 1981).

Distribution

Late Paleocene and early Eocene (Clarkforkian-Wasatchian) of the Bighorn Basin, Wyoming and possibly the Wasatchian of New Mexico (Simpson, 1931).

Discussion

Palaeanodon, well known from cranial and postcranial material (see especially Matthew, 1918; Rose, 1978) is distinguished by the fol-

lowing features: dental formula $\frac{?.1.74}{?1.1.5}$;

canines large, oval in cross-section at the base and enamel-covered; postcanines small, peglike with rounded crowns and separated by short diastemata; posterior portion of jaw edentulous; large, posteriorly-placed medial buttress and distinct internal mandibular groove present on the dentary; and bullae incomplete.

P. parvulus is distinguished from *P. ignavus* by its slightly smaller size (20–30% smaller).

***Metacheiromys* Wortman, 1903, p. 347**

Discussion

This genus is discussed in detail above (pp. 2–8).

FAMILY Epicotheriidae Simpson, 1927, p. 285

Included Genera

Epicotherium, *Xenocranium*, *Tetrapassalus*, *Pentapassalus*, *Amelotabes*, *Alocodontulum* and *Tubulodon*.

Discussion

The genera which have been included in the Epoicotheriidae (listed above) appear to form a paraphyletic group which includes both primitive forms such as *Amelotabes*, that lack any shared and derived character-states for the family, and a few advanced forms which are united relative to the metacheiromyids and plesiomorphous epoicotheriids on the basis of synapomorphies of the skull as the Epoicotheriinae (see below). Thus, as used by previous authors (e.g., Simpson, 1927; Colbert, 1942; Rose, 1978) the Epoicotheriidae has been diagnosed on the basis of shared primitive character-states, especially of the lower jaw (Rose, 1978, p. 669). Here I provisionally retain the Epoicotheriidae as a family for all of these forms; but I separate out *Xenocranium*, *Epoicotherium*, *Pentapassalus* and possibly *Tetrapassalus* as the Epoicotheriinae. The remaining genera, *Amelotabes*, *Alocodontulum*, and *Tubulodon*, are presently too poorly known to adequately assess their phylogenetic relationships and are here regarded as Epoicotheriidae incertae sedis.

SUBFAMILY Epoicotheriinae Simpson, 1927, p. 285, new rank

Included Genera

Pentapassalus, *Epoicotherium*, *Xenocranium* and possibly *Tetrapassalus*.

Discussion

The epoicotheriines are united as a clade by the following synapomorphies: extremely short and posteriorly broad skulls that are triangular in dorsal and ventral view with high and transversely wide occiputs, inflated braincases, and medium to large, ossified tympanic bullae. *Epoicotherium*, *Xenotherium*, and possibly *Tetrapassalus*, are further united by the derived character-

state of fusion of cervical vertebrae two through five.

***Pentapassalus* Gazin, 1952, p. 32**

Type Species

Pentapassalus pearci Gazin, 1952, p. 32.

Included Species

The type species and *Pentapassalus woodi* (Guthrie, 1967, p. 23).

Distribution

Early Eocene (Wasatchian), La Barge fauna, "Upper Knight beds," Sublette County, Wyoming (Gazin, 1952) and early Eocene, Lysite Member of the Wind River Formation, Fremont County, Wyoming (Guthrie, 1967).

Discussion

Gazin (1952) distinguished *Pentapassalus* by the following suite of features: dental formula $\frac{?.1.2.3}{1.1.3.3}$; teeth similar to *Tubulodon* (although note that in the two holotypes and sole known specimens of *Pentapassalus* the crown morphology is worn off) except that M_1 alone of the lower teeth is two-rooted or bilobed; P_4 and M_2 possess a single, conical root; skull short and broad (similar to *Epoicotherium*); bullae ossified, well inflated and posterior in position; and pterygoids not continuous with bullae. *Pentapassalus woodi* (originally described as a species of *Palaeonodon*, but referred to *Pentapassalus* by Rose, 1978) is distinguished from *P. pearci* by its slightly larger size (10–25% larger in most linear dimensions of the post-crania). The cheek tooth rows of *P. pearci* and *P. woodi* are the same length, but the canines in *P. woodi* are twice the size of those in *P. pearci*. As Rose (1978) noted, this is suggestive that *P. pearci* and *P. woodi* are the female and male respectively of a single species.

The holotypes of the two species of *Pentapassalus* include skulls and partial skeletons (Gazin, 1952; Guthrie, 1967; Emry, 1970; Rose, 1978, 1979). The postcranial skeleton of *Pentapassalus* is extremely similar in morphology to that of the metacheiromyids.

***Epoicotherium* Simpson, 1927, p. 285**

Synonym

Xenotherium Douglass, 1905, p. 204 (pre-occupied by *Xenotherium* Ameghino, 1904, p. 114)

Type Species

Epoicotherium unicum (Douglass, 1905, p. 204).

Included Species

The type species and possibly *Epoicotherium* sp. of Heissig (1982).

Distribution

Early Oligocene (medial Chadronian), "McCarty's Mountain," Madison County, western Montana and the White River Group in the Flagstaff Rim area of central Wyoming (Emry, 1970, 1973; Rose and Emry, 1983); possibly the early Oligocene near Pappenheim, West Germany (Heissig, 1982).

Discussion

For over 75 years only a single, nearly edentulous skull, the holotype of *Epoicotherium unicum*, had been described (Douglass, 1905; Simpson, 1927). Heissig (1982) has recently described an edentulous left mandible with five alveoli from the early Oligocene of West Germany which he assigned to "*Epoicotherium* sp." Rose and Emry (1983) subsequently described new material of *Epoicotherium* from North America including a complete skull, partial left dentary, miscel-

laneous vertebrae and the nearly complete forelimb. Comparing Heissig's (1982) description and illustration of the German specimen to Rose and Emry's (1983) description of the dentary of *Epoicotherium* confirms that Heissig may be correct in his identification, and thus this may represent the first known non-North American palaeanodont.

Epoicotherium bears an upper canine, five upper postcanines, one lower incisor, a lower canine, and five lower postcanines (Rose and Emry, 1983). Simpson (1927, p. 285) distinguished *Epoicotherium* by the following features: "depressed snout, domed occiput, slender but complete zygomata without sub- and post-orbital processes, large completely ossified tympanic bullae, with which are ankylosed the pterygoid plates, there being no hamular processes, and cylindrical, one-rooted cheek-teeth without enamel." Rose and Emry (1983) have since demonstrated that *Epoicotherium* actually bore a very thin enamel layer on at least the canines and postcanines. The axis and following three cervical vertebrae are fused in *Epoicotherium* and throughout the skeleton bears numerous subterranean, fossorial adaptations (Rose and Emry, 1983).

***Xenocranium* Colbert, 1942, p. 3**

Type Species

Xenocranium pileorivale Colbert, 1942, p. 3.

Included Species

Only the type species.

Distribution

Early Oligocene (Chadronian-?Orellan), Brule and White River Formations, White River Group, Wyoming and Nebraska (Rose, 1978; Rose and Emry, 1983).

Discussion

Xenocranium, originally described from a single skull and mandible, was distinguished by Colbert (1942, p. 3) by the following features: "much larger than *Epoicotherium*, with a depressed snout and an elevated, greatly broadened occiput; orbit without postorbital processes; bullae transversely elongated and prominent below level of the basicranium; very large, bulbous expansions of the squamosal external to the bullae and at the posterior termination of the zygomatic arch; mandible shallow, with a broad, internal shelf; teeth simple and peg-like, without enamel; five cheek teeth in the maxilla and six in the mandible, of which the anterior (canine) in each jaw is much larger than the rest of the teeth."

Rose and Emry (1983) have since redescribed the skull and mandible, and have described the anterior half of the axial skeleton and most of the forelimb of *Xenocranium*. Rose and Emry (1983) demonstrated that the dental formula of *Xenocranium* is $\frac{0.1.4}{1.1.5}$ (i.e., there is actually a small incisor anterior to the canine in the lower jaw). The snout of *Xenocranium* (missing in the holotype) is flattened and expanded anteriorly. As in *Epoicotherium*, and possibly *Tetrapassalus* (see below and Fig. 11), cervical vertebrae two through five are fused in *Xenocranium* and the skeleton is more highly specialized for subterranean, fossorial habits than in any other known palaeonodont (Rose, 1978; Rose and Emry, 1983).

Tetrapassalus* Simpson, 1959, p. 2*Type Species**

Tetrapassalus mckennai Simpson, 1959, p. 2.

Included Species

The type species and *Tetrapassalus proius* West, 1973, p. 929.

Distribution

Middle Eocene (Bridgerian) of the Bridger Formation, Bridger Basin, Wyoming.

Discussion

Tetrapassalus, described only from the two holotype partial lower dentitions and dentary fragments, is distinguished by the following features: lower canines large; cheek teeth consisting of four subequal, cylindrical, peg-like postcanines without closed roots or root division, but showing distinct occlusal wear; and posterior medial buttress slight. *T. proius* is distinguished from *T. mckennai* by its smaller size (approximately two-thirds the size of *T. mckennai*).

A maxilla and two fused cervical vertebrae series are tentatively referable to *Tetrapassalus* and are discussed below.

cf. *Tetrapassalus* sp. A**Synonymy**

cf. *Tetrapassalus* sp.: Rose, 1978, p. 672, text-fig. 5

Distribution

Middle Eocene (early Uintan) of the Tepee Trail Formation, northwestern Wyoming.

Discussion

Rose (1978) described and illustrated a right maxilla (AMNH 10215) of a small epoicotheriid which may represent *Tetrapassalus*, or perhaps more likely, a new genus and species. AMNH 10215 bears a large, pointed canine and four small, single-rooted postcanines (although the second is missing from the specimen) with enamel-covered crowns, except for the occlusal surfaces (Rose, 1978).

cf. *Tetrapassalus* sp. B

(Fig. 11)

Synonymy

?Order Edentata: Robinson, 1963, p. 6, unnumbered fig.

Epoicotheriid: West, 1973, p. 931

"fused cervical vertebrae:" McKenna, 1975, p. 29

"*Tetrapassalus* or a closely related form:" Rose and Emry, 1983, p. 42

Referred Specimens

YPM 14919, the fused centra of vertebrae two through five (Fig. 11): collected by L. LaMothe from middle Eocene-aged strata, probably upper Bridger beds, of the Bridger Formation at Lone Tree, Wyoming in 1873.

YPM 16872, a specimen identical to YPM 14919 but preserving only the centrum of the axis and part of the centrum of vertebra three (this specimen is listed by Robinson, 1963, but I have not been able to locate it in the YPM collections): collected by J. Heisey from middle Eocene-aged strata, upper Bridger beds of the Bridger Formation at Lone Tree, Henry's Fork, Bridger Basin, Wyoming, on 20 June 1874.

Discussion

The suggestions by Robinson (1963) and West (1973) that YPM 14919 and YPM 16872 represent the fused cervical vertebrae of an epoicotheriid are corroborated by the recent description of fused cervical vertebrae in *Epoicotherium* and *Xenocranium* by Rose and Emry (1983, p. 42) who refer YPM 14919 and YPM 16872 to "*Tetrapassalus* or a closely related form" on the basis of size. The cervicals are unfused in the metacheiromyids (e.g., see Fig. 11, J; the axis of *Metacheiromys marshi*).

Type Species

Amelotabes simpsoni Rose, 1978, p. 660.

Included Species

Only the type species.

Distribution

Late Paleocene (Tiffanian) of the Bighorn Basin, Wyoming.

Discussion

Amelotabes simpsoni, known from a single dentary and partial lower dentition, is distinguished by the following features: mandible shallow, robust with medial buttress and internal mandibular groove; dental formula $\frac{?.?.?.?}{?1.1.4.3}$; canines large; P₁ single-rooted; P₂-M₃ double-rooted; cheek teeth with thin enamel on occlusal surfaces; P₂₋₃ with large protoconids, small, low paraconids and slight protocristsids; P₃ with small talonid heel; molars with primitive eutherian cusp pattern; molars low crowned with bulbous and poorly defined cusps; protoconids largest and highest cusps on the molars; and hypoconulids, cristsids obliquae and cingulids absent.

Alocodontulum* Rose, Bown and Simons, 1978, p. 1162*Synonymy**

Alocodon Rose, Bown and Simons, 1977, p. 1 (preoccupied by *Alocodon* Thulborn, 1973, p. 93)

Type Species

Alocodontulum atopum (Rose, Bown and Simons, 1977, p. 2).

Included Species

Only the type species.

Epoicotheriidae Incertae Sedis

Amelotabes Rose, 1978, p. 659

Distribution

Early Eocene, upper "Gray Bull" beds, lower Willwood Formation, Bighorn Basin, Wyoming.

Discussion

Alocodontulum is known only from the genoholotype, an incomplete premaxilla-maxilla and partial upper dentition. Rose, Bown and Simons (1977, p. 2) diagnosed this taxon as follows: "Upper molars longer than wide, and uniquely specialized; M^{1-2} with median longitudinal furrow, several cusps arranged in line on lingual and buccal borders of crown, and no enamel on top of crown. M^1 slightly larger than M^2 , both much larger than M^3 ; M^3 greatly reduced, single-rooted, with very low and bulbous crown. P^3 premolariform, with large paracone, rudimentary metacone, small low protocone. P^{1-2} tiny, single-rooted. Canine of moderate size, triangular in section."

Rose, Bown and Simons (1977) assigned *Alocodontulum* to the Epoicotheriidae primarily on the basis of the following similarities that it shows to either *Pentapassalus* or *Tubulodon* or to both: enamel reduction on the teeth (occlusal surfaces of the cheek teeth lack enamel); similar scalloped margins on the molars of *Alocodontulum* and *Tubulodon*; upper molars longer than wide; M^3 peg-like; and upper canine triangular in cross section with the anteromedial face honed and lacking enamel.

Tubulodon* Jepsen, 1932, p. 264*Type Species**

Tubulodon taylori Jepsen, 1932, p. 264.

Included Species

Only the type species.

Distribution

Late early Eocene (Lostcabinian) of the Lost Cabin Member, Wind River Formation, Wind River Basin, Wyoming.

Discussion

Originally thought by Jepsen (1932) to be related to the extant aardvark (*Orycteropus*, Tubulidentata), *Tubulodon*, known only from partial lower dentitions (Jepsen, 1932; Guthrie, 1971) is distinguished by the following features: cheek teeth similar to those of *Amelotabes* with low and marginally situated cusps; three lower molars present (P_4 only known premolar); known teeth double-rooted with hypsodont, columnar crowns; cheek teeth with thin enamel on the sides and lacking enamel on the occlusal surfaces. The genoholotype of *Tubulodon* has microscopic tubules present in the teeth and Jepsen (1932) considered these tubules to indicate a relationship to the Tubulidentata. Colbert (1941) argued that the tubules seen in *Tubulodon* are unlike those seen in *Orycteropus* and allies, whereas both Gazin (1952) and Rose, Bown and Simons (1977) have observed similar tubules in the teeth of other Eocene mammals. Rose, Bown and Simons (1977; cf. Peyer, 1968) note that dentine tubules are present in the teeth of most mammals and these authors suggest that tubules may merely be more readily seen in some fossil mammals in which the enamel is thin (e.g., *Tubulodon*, *Alocodontulum* and *Pentapassalus*).

Conclusions

Fourteen species, ten genera, three subfamilies and two families are formally recognized within the order Palaeanodonta (Table 3). The earliest known palaeanodonts are *Amelotabes* and *Propalaeanodon*, both from the Tiffanian of the Bighorn Basin, Wyoming. Whereas *Amelotabes* appears to be the most primitive known palaeanodont, and may thus approximate the ancestral palaeanodont morphotype, *Propalaeanodon* bears derived metacheiromyid features. The latest and most derived palaeanodonts are *Epoicotherium* and *Xenotherium* from the early Oligocene. Traditionally the Palaeanodonta have been regarded as a wholly North American group; however, the recent referral of a specimen from the early Oligocene of West Germany to *Epoicotherium* sp. (Heissig, 1982) suggests that further collecting may extend the geographic and stratigraphic range of this poorly known mammalian order.

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Table 3

A classification of the Palaeanodonta.

Order Palaeanodonta
Family Metacheiromyidae
Subfamily Propalaeanodontinae
<i>Propalaeanodon</i> (1 species)
Subfamily Metacheiromyinae
<i>Palaeanodon</i> (2 species)
<i>Metacheiromys</i> (2 species)
Family Epoicotheriidae
Subfamily Epoicotheriinae
<i>Pentapassalus</i> (2 species)
<i>Epoicotherium</i> (1 species)
<i>Xenocranium</i> (1 species)
<i>Tetrapassalus</i> (2 species)
Epoicotheriidae incertae sedis
<i>Amelotabes</i> (1 species)
<i>Alocodontulum</i> (1 species)
<i>Tubulodon</i> (1 species)

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Fig. 1 ▶

Metacheiromys marshi, all figures approximately $\times 2$: A) stereophotographic pair, occlusal view, YPM 12903, left dentary (lectotype), length 30.8; B) labial view, YPM 12903, left dentary; C) lingual view, YPM 12903, left dentary; D) stereophotographic pair, labial view, YPM 13502, posterior fragment of left dentary, maximum preserved height 12.9; E) labial, YPM 12903, right maxillary fragment with canine, maximum preserved length 17.0; F) lingual view, YPM 12903, right maxillary fragment with canine; G) labial view, YPM 12903, left canine, length 11.7; H) lingual view, YPM 12903, left canine; I) stereophotographic pair, dorsal view, YPM 12903, axis, width 12.4; J) stereophotographic pair, ventral view, YPM 12903, axis; K) stereophotographic pair, distal view, YPM 12903, glenoid cavity of right scapula, height 9.5; L) stereophotographic pair, lateral view, YPM 12903, partial right scapula; M) stereophotographic pair, medial view, YPM 12903, partial right scapula.

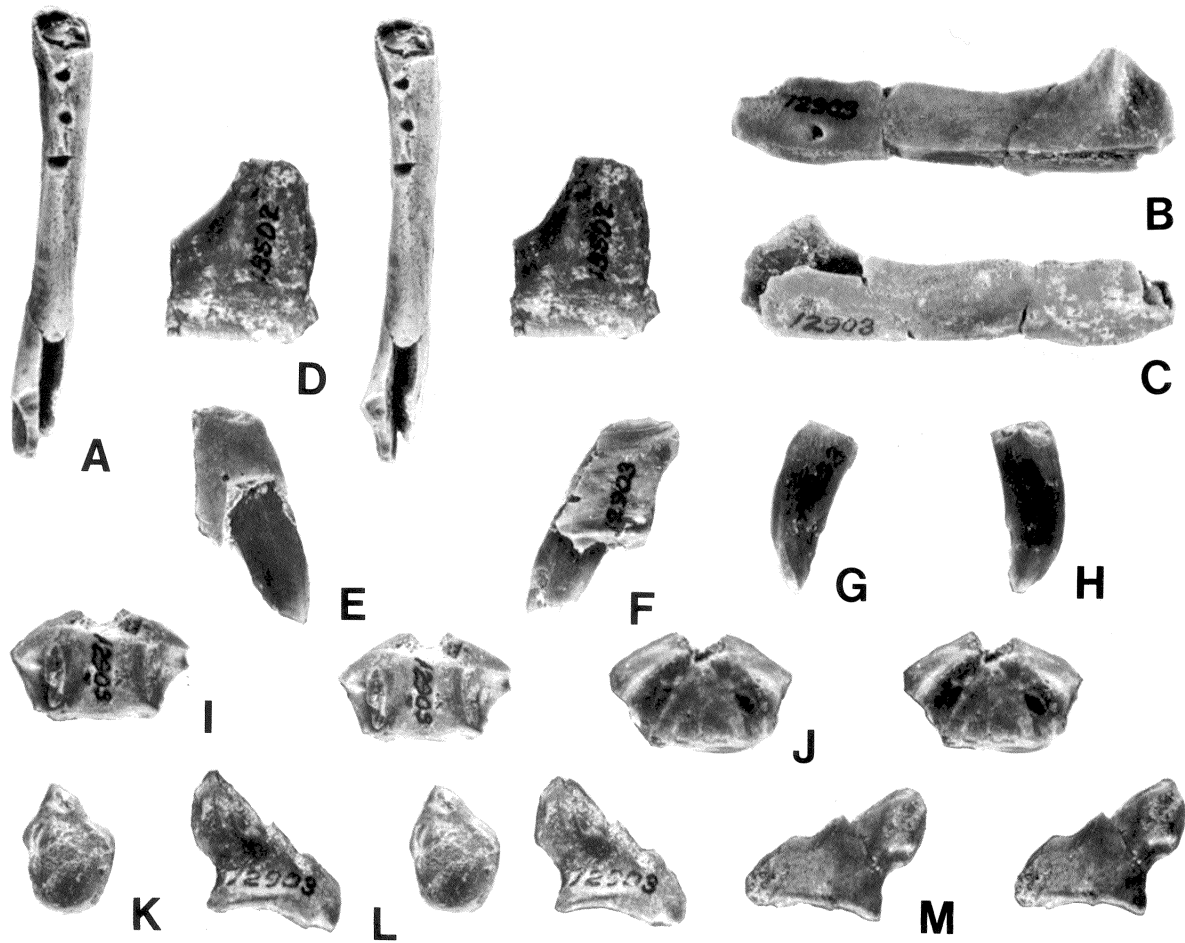


Fig. 2 ►

Metacheiromys marshi, all figures approximately $\times 2$: *A*) stereophotographic pair, anterior view, YPM 12903, proximal end of right humerus, maximum width 12.3; *B*) stereophotographic pair, anterior view, YPM 12903, distal end of right humerus, maximum width 21.1; *C*) stereophotographic pair, posterior view, YPM 12903, proximal end of right humerus; *D*) stereophotographic pair, posterior view, YPM 12903, distal end of right humerus.



Fig. 3 ▶

Metacheiromys marshi, all figures approximately $\times 2$: *A*) lateral view, YPM 12903, distal end of right ulna, maximum preserved length 36.0; *B*) medial view, YPM 12903, distal end of right ulna; *C*) stereophotographic pair, anterior view, YPM 12903, distal end of right ulna; *D*) stereophotographic pair, medial view, YPM 40067, left ulna, length 46.1; *E*) stereophotographic pair, anterior view, YPM 40067, left ulna.

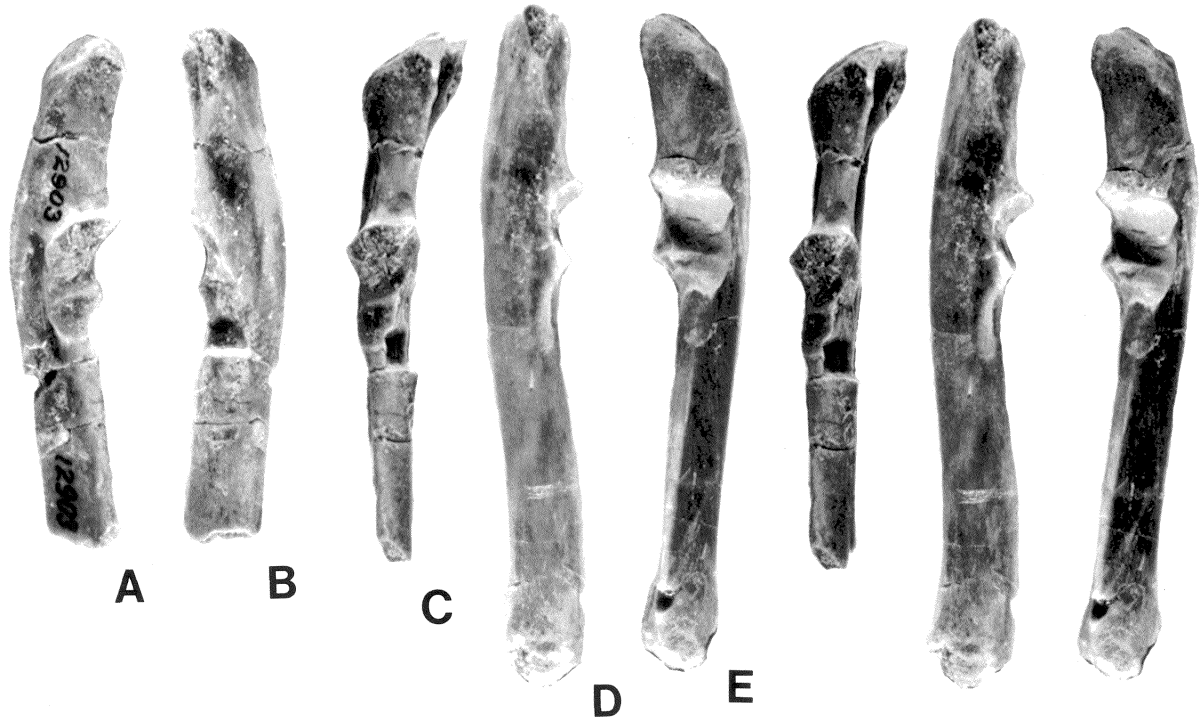


Fig. 4 ▶

Metacheiromys marshi, all figures approximately $\times 2$: A) stereophotographic pair, distal view, YPM 13502, distal end of left femur, width 14.2; B) stereophotographic pair, proximal view, YPM 13500, proximal end of left femur, width 14.4; C) stereophotographic pair, anterior view, YPM 13500, proximal end of left femur; D) stereophotographic pair, anterior view, YPM 13502, distal end of left femur; E) stereophotographic pair, posterior view, YPM 40067, proximal end of left radius, maximum preserved length 13.5; F) stereophotographic pair, lateral view, YPM 40067, proximal end of left radius; G) stereophotographic pair, posterior view, YPM 13500, proximal end of left femur; H) stereophotographic pair, posterior view, YPM 13502, distal end of left femur.

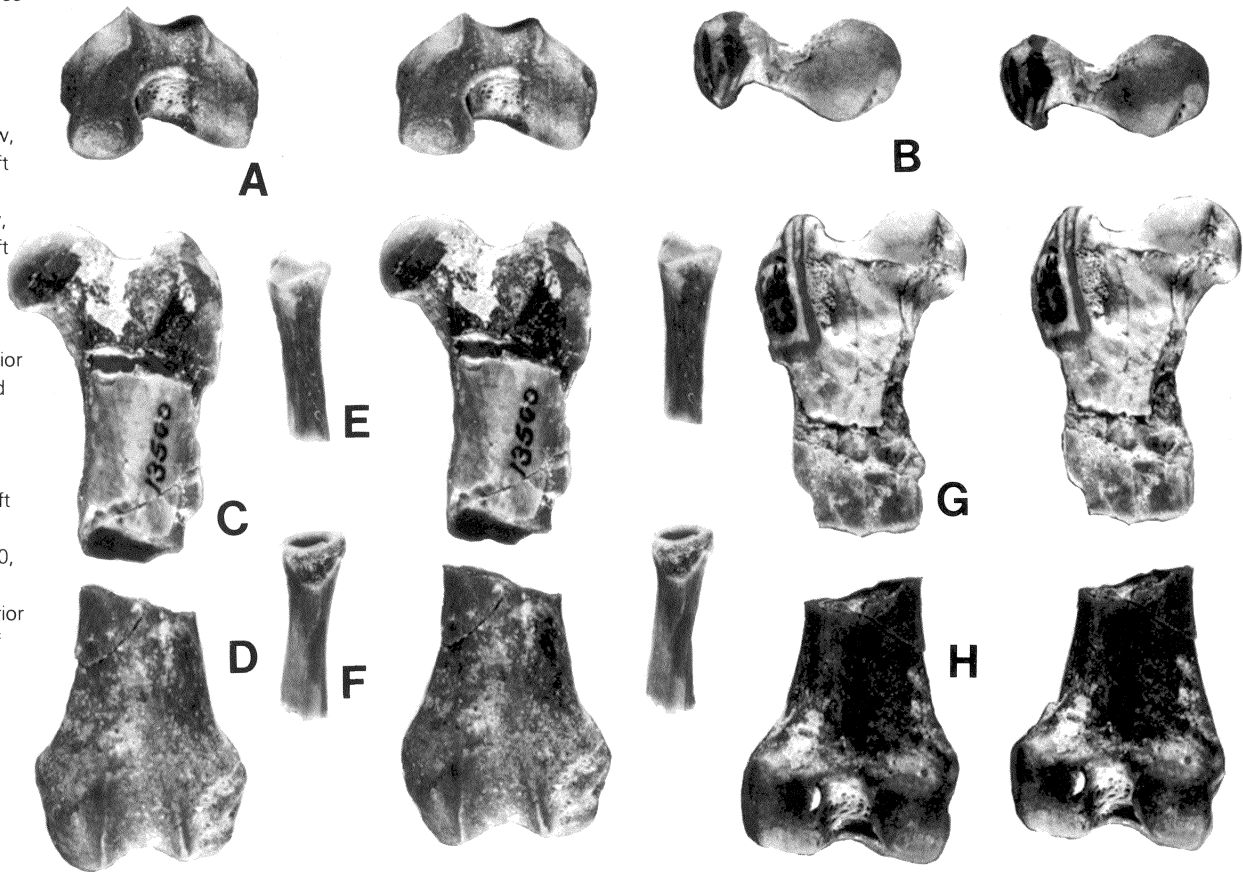


Fig. 5 ▶

Metacheiromys marshi, all figures approximately $\times 2$: A) stereophotographic pair, anterior view, YPM 13501, proximal end of right tibia, width 13.0; B) stereophotographic pair, anterior view, YPM 13501, distal end of left tibia, width 10.9; C) stereophotographic pair, posterior view, YPM 13501, proximal end of right tibia; D) stereophotographic pair, posterior view, YPM 13501, distal end of left tibia; E) stereophotographic pair, proximal view, YPM 13501, proximal end of right tibia; F) stereophotographic pair, distal view, YPM 13501, distal end of left tibia.

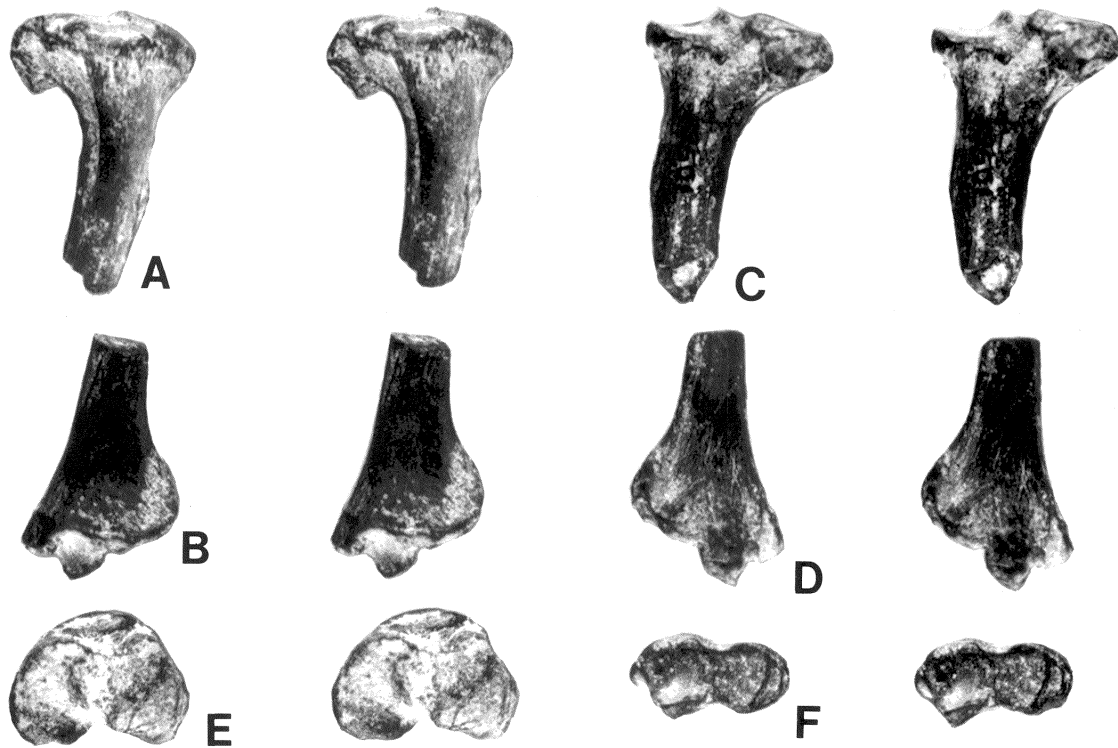


Fig. 6 ▶

Order Primates, genus and species indeterminate, all figures approximately $\times 2$: *A*) stereophotographic pair, proximal view, YPM 12903, proximal end of right tibia, width 14.9; *B*) stereophotographic pair, distal view, YPM 12903, distal end of right tibia, width 9.4; *C*) stereophotographic pair, anterior view, YPM 12903, proximal end of right tibia; *D*) stereophotographic pair, anterior view, YPM 12903, distal end of right tibia; *E*) stereophotographic pair, posterior view, YPM 12903, proximal end of right tibia; *F*) stereophotographic pair, posterior view, YPM 12903, distal end of right tibia.

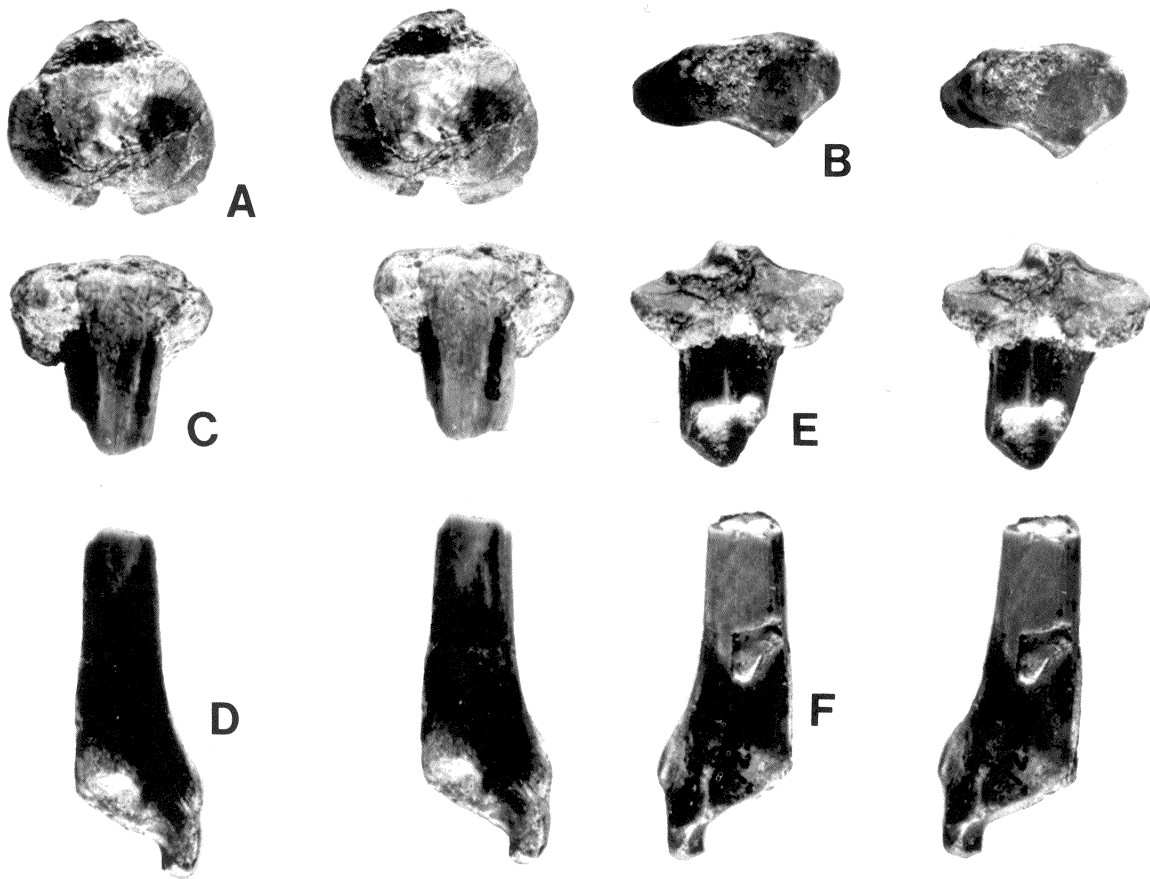


Fig. 7 ▶

Order Primates, genus and species indeterminate (*B*) and *Metacheiromys marshi* (*A, C*), all figures approximately $\times 2$: *A*) stereophotographic pair, lateral view, YPM 13503, right ilium and acetabular part of pelvis, length 44.3; *B*) stereophotographic pair, lateral view, YPM 12903, right acetabular part of pelvis, maximum preserved length 21.9; *C*) stereophotographic pair, ventral view, YPM 13503, sacrum, maximum preserved length 27.8.

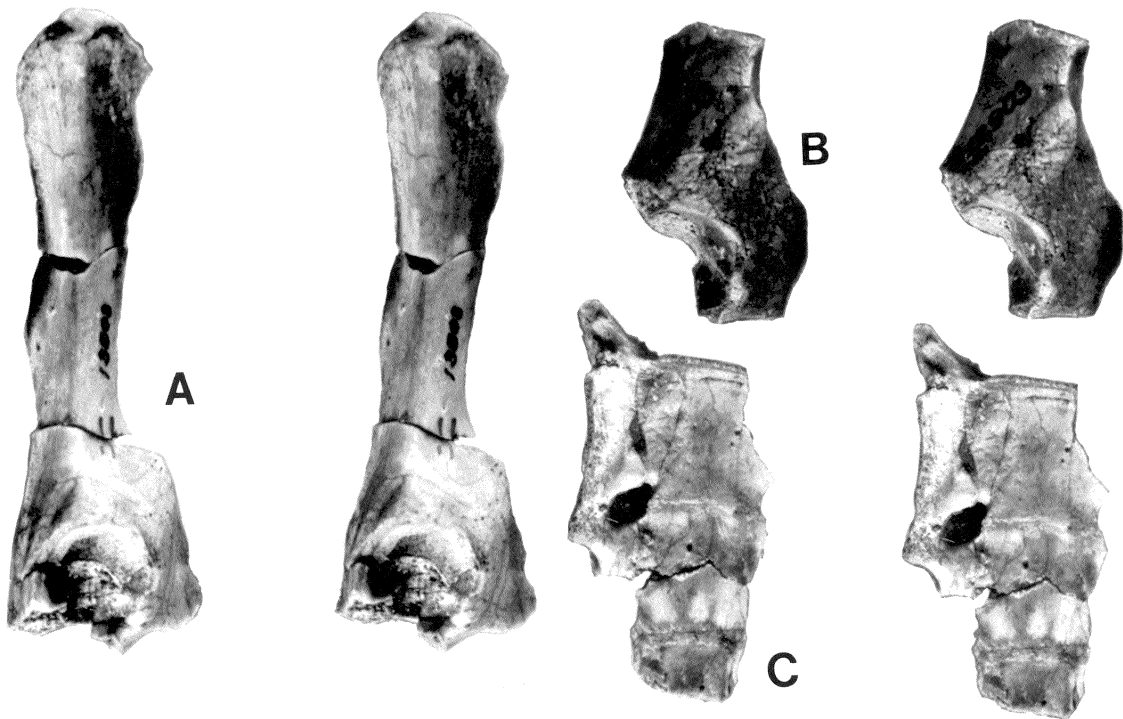


Fig. 8 ▶

Metacheiromys marshi, all figures approximately $\times 2$ except C which is approximately $\times 1.5$: A) stereophotographic pair, dorsal view, YPM 13501, partial right pes, maximum preserved length 31.1; B) stereophotographic pair, ventral view, YPM 13501, partial right pes; C) stereophotographic pair, dorsal view, YPM 13502, sacrum, left ilium and acetabular part of pelvis, maximum preserved length 47.0; D) stereophotographic pair, dorsal view, YPM 13501, first phalanx of undetermined digit of pes, length 6.5; E) stereophotographic pair, dorsal view, YPM 13501, second phalanx of undetermined digit of pes, length 4.3; F) stereophotographic pair, side view, YPM 13501, ungual phalanx of undetermined digit of ?manus, length 11.7.

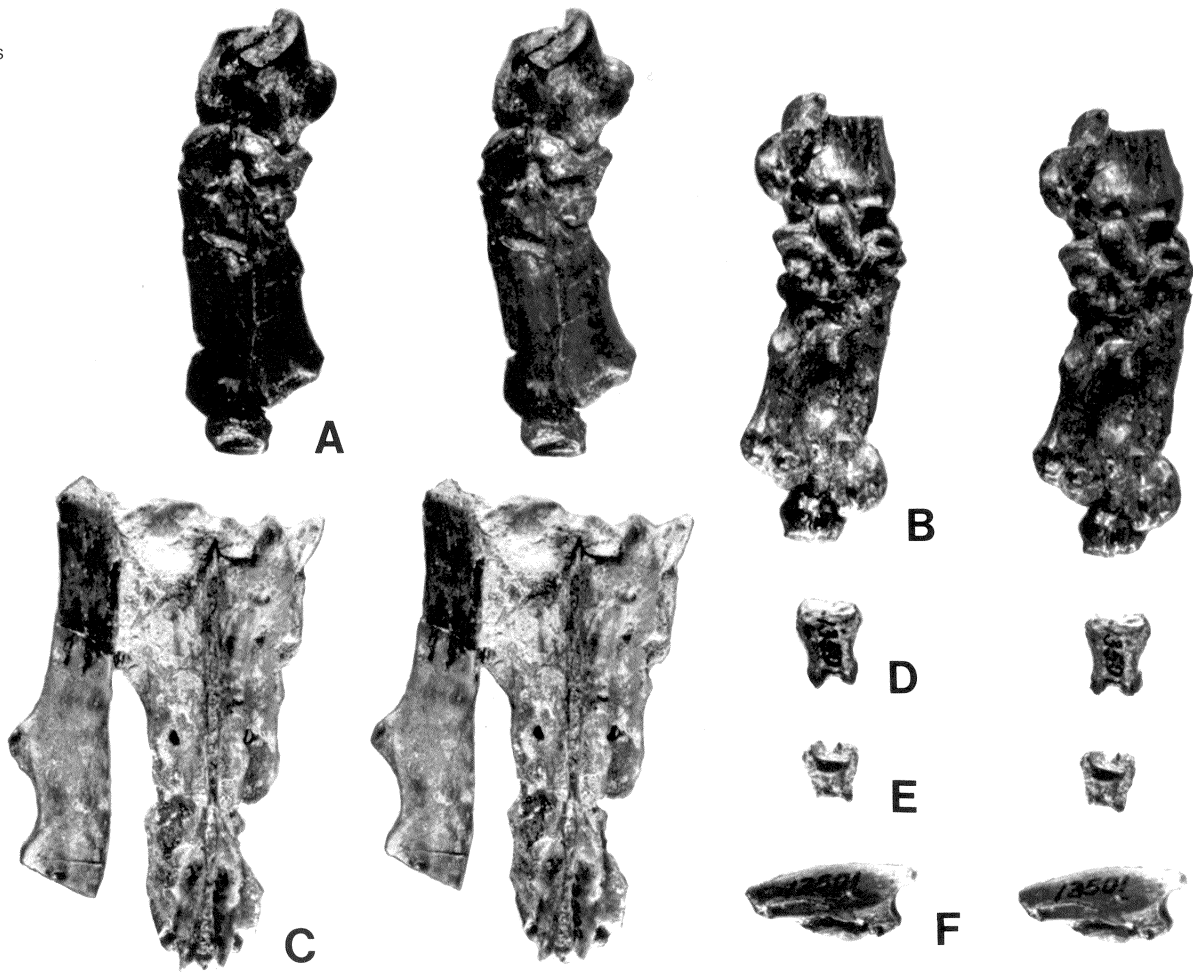


Fig. 9 ▶

Metacheiromys marshi, approximately $\times 1.45$: ventral view, YPM 13501, left ischium and first seven caudal vertebrae, length of first seven caudals 61.4



Fig. 10 ▶

Metacheiromys dasypus, all figures approximately $\times 2$: *A*) stereophotographic pair, dorsal view, YPM 40068, right astragalus, maximum diameter of head 8.8; *B*) stereophotographic pair, dorsal view, YPM 40068, right cuboid, maximum length 12.0; *C*) stereophotographic pair, ventral view, YPM 40068, right astragalus; *D*) stereophotographic pair, medial view, YPM 40068, right cuboid; *E*) stereophotographic pair, dorsal view, YPM 40069, first phalanx of second digit of left pes, length 10.5; *F*) stereophotographic pair, ventral view, YPM 40069, first phalanx of second digit of left pes.

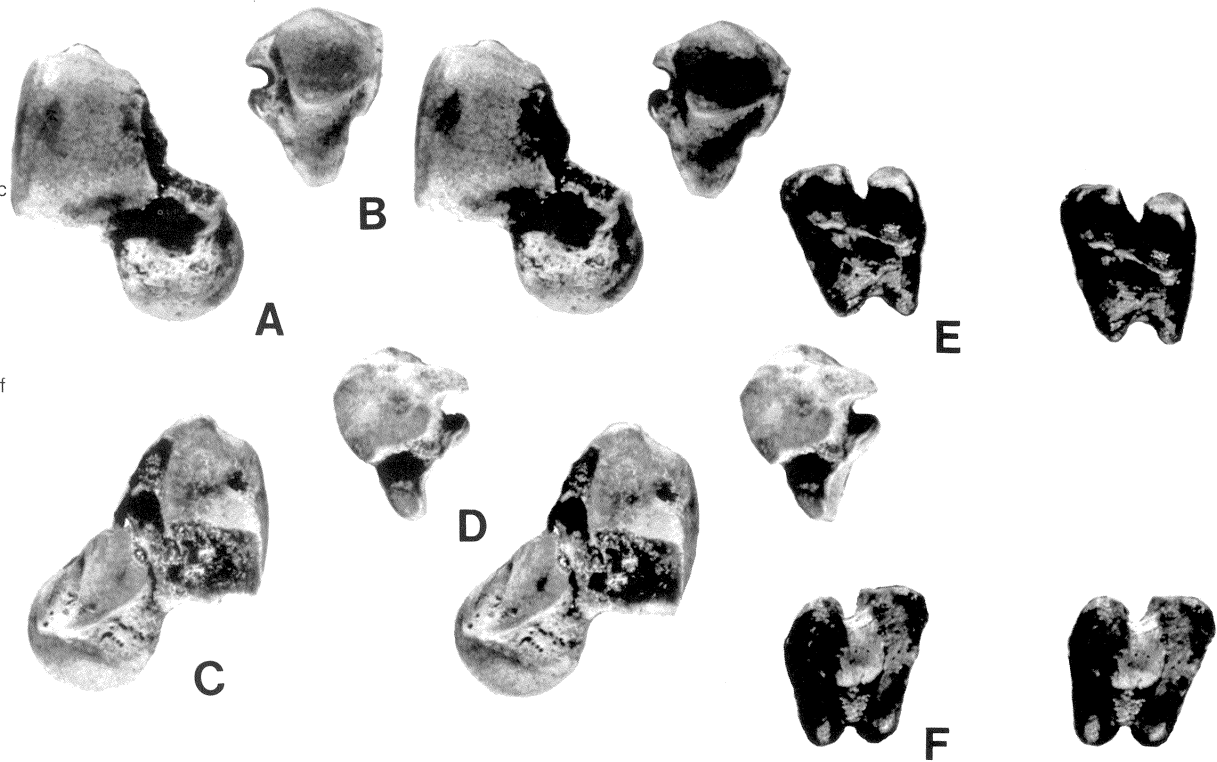
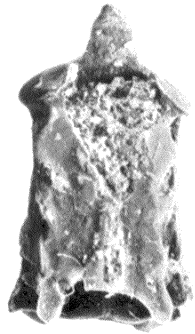
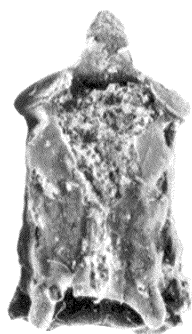


Fig. 11 ▶

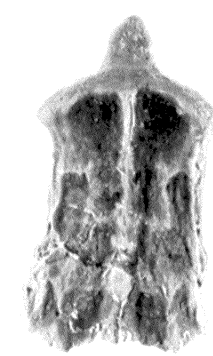
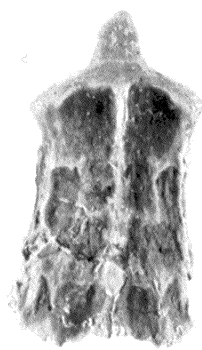
cf. *Tetrapassalus* sp. B, YPM 14919, fused centra of cervical vertebrae two (axis) through five, maximum length 11.6, all figures approximately $\times 4$: *A*) stereophotographic pair, dorsal view; *B*) stereophotographic pair, ventral view; *C*) stereophotographic pair, right lateral view; *D*) stereophotographic pair, left lateral view; *E*) stereophotographic pair, anterior view; *F*) stereophotographic pair, posterior view.



A



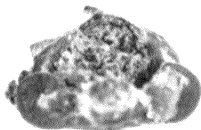
B



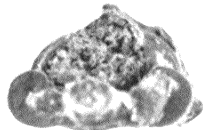
C



D



E



F

