Article VI.—METACHEIROMYS AND THE EDENTATA

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23 Text Figures

CONTENTS

INTRODUCTION

In 1903 a field party of The American Museum of Natural History under the leadership of Walter Granger discovered two primitive mammal skeletons in the Middle Eocene Bridger Formation of Wyoming. One of these, better exposed in the field, was at once recognized as an edentate by Mr. Granger, who announced its discovery to Professor Osborn in a letter dated June 21, 1903.

In the meantime, Dr. J. L. Wortman had been engaged in the study of the Eocene mammals in the Marsh Collection in the Peabody Museum of Yale University. In November, 1903 (see references), he published a notice of the new genus and species *Metacheiromys marshi*, based on skull fragments, a mandibular ramus, some vertebræ and ribs, and parts of scapula, humerus, ulna, pelvis, and tibia. His conclusion as to affinities was that *Metacheiromys* was a primate closely related to the living *Cheiromys*. Reference to the Primates was largely due to the evidence of a tibia which "has every mark and feature of the Primate so unmistakably stamped upon it that I have no hesitancy in referring the species to this order. . . . " Further, "Is it possible to suppose that these modifications [i.e., acquisition of supposed gliriform incisors], so profound and unique among the Primates, have originated twice in the same group entirely independently of each other?" This argument rests primarily on the tibia, however, and it is now known that this was incorrectly associated with the jaw fragments. It belongs to one of the true Bridger primates, and that of *Metacheiromys* is very different.

Upon preparing the 1903 collection, it was apparent that the American Museum edentate was the same as Wortman's supposed "cheiromyoid." On May 10, 1904, Professor Osborn published a brief unillustrated account of the two most complete new specimens, giving to them the names *Metacheiromys dasypus* and *M. tatusia*, the former being much larger, the latter slightly smaller, than *M. marshi*. His general conclusions regarding the structure and affinities of *Metacheiromys* were given in the following words:

"Closely similar in its general osteology to *Tatusia* and *Dasypus*, but exhibiting a number of more primitive characters, such as free cervicals, more equal sternal segments, fore and hind limbs approximately equal in length, tibia and fibula separate; and certain more specialized characters, such as wide curvature of ulna, elongation of the deltopectoral crest of humerus. Still more widely specialized is the dentition, which is practically abortive except for the tusk-like upper and lower canines which are covered with enamel. These at first sight suggest the tusks of the sloth *Cholæpus*, but the lower tooth is apparently homologous

with the canine. The most striking general feature is the extreme modernization of the skeleton; it lacks only the compound articulation of the dorsal vertebræ and the presence of ossicles in the dermal shield to be described as a fully developed Armadillo."

In 1910 a photograph of the mounted skeleton of *Metacheiromys tatusia* was published (Osborn 1910, p. 164, Fig. 64). This, with the earlier notice, has prevented the inclusion of *Metacheiromys* among primates, but has not won it proper attention in its rightful position.

In 1918 W. D. Matthew described a related genus, *Palæanodon*, from the Clark Fork and Lower Eocene horizons of Wyoming, erecting for this genus and *Metacheiromys* the new suborder Palæanodonta. The Middle Eocene forms were incidentally mentioned, but not described in further detail. Osborn's view as to their edentate affinities was confirmed and strengthened by much detailed evidence. Matthew concluded that "it is convenient to rank it [*Metacheiromys*] for the present in a distinct suborder, whose relations to the Loricata are, I suspect, much like those of the creodonts to the fissipede Carnivora. The only family at present known is the Metacheiromyidæ, which, like the hyænodonts, oxyænids or mesonychids among the Creodonta, is an aberrant side branch, although primitive in most features, and affords important clues as to the derivation and affinities of the Xenarthra and Pholidota."

"Save for the reduction of the cheek teeth and the supposed character of the canines (the last inferred from the near relationship to *Metacheiromys*), I see nothing in the skeleton structure against regarding *Palæanodon* as a direct ancestor of the South American Tertiary and modern Loricata, or indeed of all the Xenarthra." "On the whole I can find no very conclusive evidence against deriving *Manis* as well as the Loricata (and through them the remaining Xenarthra) from the primitive type represented by *Palæanodon*. Just how direct the ancestors may be in each case is a highly speculative matter."

Knowledge of *Palæanodon*, although not so complete as that of *Metacheiromys*, includes much of the skeleton, and this genus was fully described, illustrated, and discussed by Matthew. Even this work, however, has not yet made much impression on the general field of fossil mammalogy—it is not mentioned, for instance, in the last edition of the classic Schlosser–Zittel "Grundzüge."

. Such further discussion of *Metacheiromys* or *Palæanodon* as does occur in the literature is largely expressive of doubt. Ameghino (1905) signalized *Metacheiromys* as extraordinary and suspended judgment, although suggesting affinity with the European fossil supposed edentate *Galliætatus*.
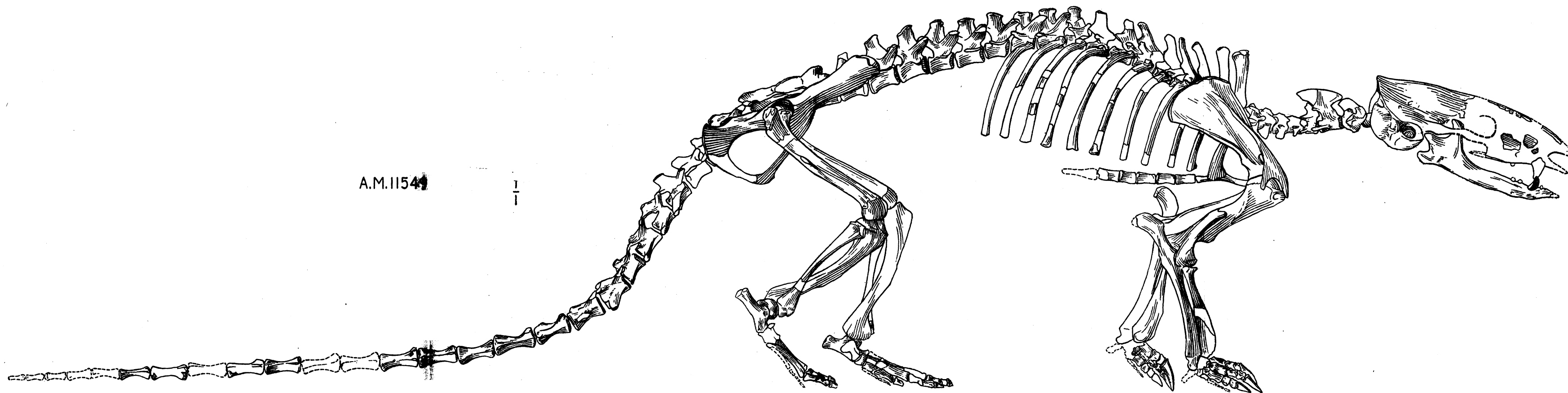
A.M.11549

Fig. 1. *Metacheiromys tatusia* Osborn. Complete skeleton, type, Amer. Mus. No. 11549. Parts restored from other specimens in outline, hypothetical parts dotted. Natural size.

Scott (1913, pp. 616–617) concluded that "while these curious animals may very possibly have been referable to the Edentata and, at all events, had several features suggestive of relationship to that order, it can hardly be maintained that they were unequivocal members of it." Stehlin, discussing Eocene primates (1916, p. 1504), rejected *Metacheiromys* as a primate. "Dass das, von Wortman aufgestellte, Genus *Metacheiromys* aus der Bridger-Stufe weder mit unsern europäischen Formen [plesiadapids and their allies] noch mit *Chiromys* etwas zu thun hat, ist auch ohne die ergänzenden Mittheilungen die Osborn über dasselbe gemacht hat, evident."

Winge, whose almost universal knowledge of the literature of fossil mammals went far to counteract his lack of autoptic study, did not ignore the work of Osborn and Matthew. In his study of Lagoa Santa edentates (1915, p. 307) he expressed a belief that *Metacheiromys* probably had nothing to do with the edentate stock. For his final expression of opinion (1923, pp. 343–344) he had the more complete documentation of Matthew's study of *Palæanodon*, but still strongly opposed Osborn's and Matthew's beliefs.

Winge's point of view is summed up in the following free translation of part of his discussion:

"In the skeleton there are, indeed, many extraordinary similarities to the armadillos. Among the most peculiar in this respect is the way in which the stoutest phalanges articulate with the corresponding metapodials and with each other, but the value of this resemblance is almost negatived by the fact that in *Palæanodon* and *Metacheiromys* there is no trace of the dissimilarity in length and strength between the inner and outer digits which occurs in the armadillos. Similarly, in other respects the resemblances are counteracted by differences. It is quite incredible that the peculiar characters of the armadillos should have developed independently of each other to such a degree that edentates with enameled teeth, with unfused cervicals, normal trunk vertebræ and sternum, with the pelvis free of the caudals, with digits of normal proportions, without a shield, etc., should be on as high a level as the most advanced armadillos in other characters, in reduction of the teeth, in peculiarities of the phalangeal articulations, etc."[1]

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[1] "I skelettet findes ganske rigtig mange paafaldende Ligheder med Beltedyr; noget af det mest ejendommelige i denne Henseende er den Maade, hvorpaa de Stærkeste af Fingerleddene ere indtrykke i de tilsvarende Mellemhaandsben og i hinanden indbyrdes; men denne Overensstemmelses Værd bliver nærmest ophævet af, at der hos *Palæanodon* og *Metacheiromys* ikke findes Spor af den Ulighed i Længde og Sværhed mellem de indre og ydre Fingre, der findes hos Beltedyr; og paa lignende Maade gaar det i andre Henseender; Lighederne ophæves af Uligheder. Det er ikke ret troligt, at Beltedyrenes Egenheder skulle være komne i den Grad uafhængig af hverandre, saa at Gumlere med emaillekklædte Tænder, med frie Halshvirvler, normale Ryghvirvler og Brystben, med Bækkebenet frit fra Halehvirvler, med Fingre af sædvanlige Störrelse-Forhold, uden Skjold, o.s.v., allerede i andre Henseender skulde staa paa Höjde med de överste Beltedyr, i Kindtændernes Vanslægtning, i Egenheder i Fingerled. o.s.v. . . ."

Winge accordingly omits these genera from his classification and from the body of his text. Although he thus finds the Palæanodonta too unevenly specialized to serve as structurally ancestral to other edentates, he strangely does not experience the same difficulty with the orycteropodids, which occupy this central position of his scheme.

Abel (1922, pp. 291–293) accepted the view of Osborn and Matthew regarding the relationships of *Metacheiromys* and discussed its zoögeographic significance.

As already mentioned, Schlosser (1923, p. 505) omits all mention of the more completely published *Palæanodon* and concludes only that "Die reduzierte Bezahnung $\frac{}{1.1.2}$ von *Metacheiromys*. Wortman aus dem Bridgereocän von Wyoming lässt sich schwer mit der Annahme Osborn's vereinbaren, wonach diese Reste einem panzerlosen Dasypodiden angehören sollen. Immerhin ist eine sehr entfernte Verwandtschaft mit diesen nicht vollkommen ausgeschlossen."

The recent second edition of Weber's "Säugetiere" (1928) gives an adequate résumé of Matthew's views.

Professor Osborn planned a definitive description of *Metacheiromys* and had some wash drawings prepared, but these were subsequently placed in Dr. Matthew's hands. The latter referred to *Metacheiromys* in his study of *Palæanodon*, but did not carry farther the publication of the Middle Eocene specimens. It is the generosity of these two authorities in relinquishing this important material, which both have critically studied, that makes possible its publication at this time. Although the present study inevitably largely confirms their views, published and unpublished, it has been independently prosecuted. Indebtedness to Walter Granger and Albert Thomson, who collected and prepared the two wonderful skeletons here described, is also gratefully acknowledged.

I am further indebted to Professor R. S. Lull and to Dr. M. R. Thorpe of the Peabody Museum, Yale University, for facilitating study of Wortman's type material and for lending important specimens hitherto undescribed.

The drawings in this paper are by John Germann.

TAXONOMY

Palæanodonta Matthew, 1918

DEFINITION.—"Ancestral edentates with nomarthrous vertebræ, no ischio-caudal symphysis, canine teeth present and enamel bearing, no calcified dermal shield, otherwise as in Loricata, but less specialized than the Miocene and later members of that group." (Matthew, 1918, p. 620; type definition).

DISTRIBUTION.—Clark Fork to Upper Bridger, Western United States.

METACHEIROMYIDÆ Wortman, 1903; Matthew, 1918

DEFINITION.—"Upper and lower canines sharp, compressed, laniary, post-canine teeth reduced or absent, a horny plate probably replacing them. No incisors. [At least one lower incisor in both genera, G. G. S.] Fore and hind feet armadilloid in type, with four or five digits on manus and pes, the lateral digits reduced, the inner possibly vestigial." (Matthew, 1918, p. 621. No definition given by Wortman). Sole known family of the order.

TYPE.—*Metacheiromys* Wortman.

DISTRIBUTION.—As for Palæanodonta.

PALÆANODON Matthew, 1918

DEFINITION.—"Cheek teeth small, one-rooted, but less reduced than in *Metacheiromys*." (Matthew, 1918, p. 621; type definition). Five lower cheek teeth. Bullæ incomplete. Structure generally more primitive than in *Metacheiromys*.

TYPE.—*P. ignavus* Matthew.

REFERRED SPECIES.—*P. parvulus* Matthew.

DISTRIBUTION.—Clark Fork (*P. parvulus*), Graybull (*P. ignavus*), probably Lysite (*P. ignavus*), perhaps also Lost Cabin (*?Palæanodon* sp. indet.), of Wyoming, and ?Largo (*?Palæanodon* sp. indet.) of New Mexico.

Fig. 2. *Palæanodon ignavus* Matthew. Part of right lower jaw. E. L. Troxell Collection, No. 140. A, Superior view. B, External view. Natural size.

A new specimen (T140) found by E. L. Troxell in 1929 in the Wasatch Formation 12 miles west of Basin, Wyoming, adds somewhat to the knowledge of this genus, and is available for notice and illustration here through the kindness of Dr. Troxell. The specimen consists of the anterior part of the right lower jaw and is referable to *Palæanodon ignavus* Matthew.

This part of the jaw resembles that of *Metacheiromys* rather closely save for the number of teeth. Matthew states that there are no incisors in the Metacheiromyidæ, but as will be shown below there is one lower incisor in *Metacheiromys*. In *Palæanodon* there was also at least one lower incisor, for the posterior edge of its alveolus is preserved in the present specimen. It is somewhat procumbent and was probably over 1 mm. in diameter. The canine is similar to that of

Metacheiromys but its base is oval, rather than distinctly triangular. The anteroposterior diameter of the alveolus is 4.5 mm. The posterior face of the crown has a deep wear facet. The enamel is much corroded in the fossil but apparently was present, and what I take to be traces of it remain.

Four cheek tooth alveoli and the anterior margin of a fifth are preserved. It seems fairly certain that the latter is the last from comparison with Amer. Mus. No. 16831, in which the last alveolus is present. In the upper jaw of Amer. Mus. No. 15086, there are four alveoli, with a possibility of others anterior to them. The third from the back is the largest. In the lower jaw the third from the front is the largest. These facts rather definitely fix five as the number of lower cheek teeth, although not all are completely preserved on any one specimen. These are evenly spaced with short diastemata between them. Each alveolus is oval, the following being the greatest, anteroposterior, diameters at the mouths of the first four.

1–0.9 mm.
2–1.6
3–1.8
4–1.7

The broken base of the fourth cheek tooth, the only one preserved, consists of homogeneous dentine, now black, with a minute pulp cavity.

There are three mental foramina, the largest beneath the first cheek tooth, the second higher and between the second and third cheek teeth, and the third, smallest, still higher and beneath the third cheek tooth.

METACHEIROMYS Wortman, 1903

DEFINITION.—Dental Formula $\frac{0}{1}\cdot\frac{1}{1}\cdot\frac{1}{2}$. Canines large, other teeth vestigial. Much longer part of jaws edentulous than in *Palæanodon*. Shelf for lower horny plate not grooved, narrower, less conspicuous. Ossified bullæ complete. Generally more advanced in structure.

TYPE.—*M. marshi* Wortman.

DISTRIBUTION.—Bridger Formation, Wyoming.

Palæanodon is definitely known to occur in the Clark Fork and Gray Bull, and probably also in the Lysite. From the latest Lower Eocene (Lost Cabin) a number of skeletal parts are known which are intermediate between *Palæanodon* and *Metacheiromys* in character. These have been described by Matthew (1918, pp. 641–643). In the absence of skull or jaw parts he refrained from applying specific names or making definite generic reference, placing them in *Palæanodon* with a query.

Four species of *Metacheiromys* are known. Although also differing in other respects, these may be most readily recognized from their relative dimensions, *M. tatusia* being the smallest, *M. marshi*, *M. dasypus*, and *M. osborni* larger in the order named.
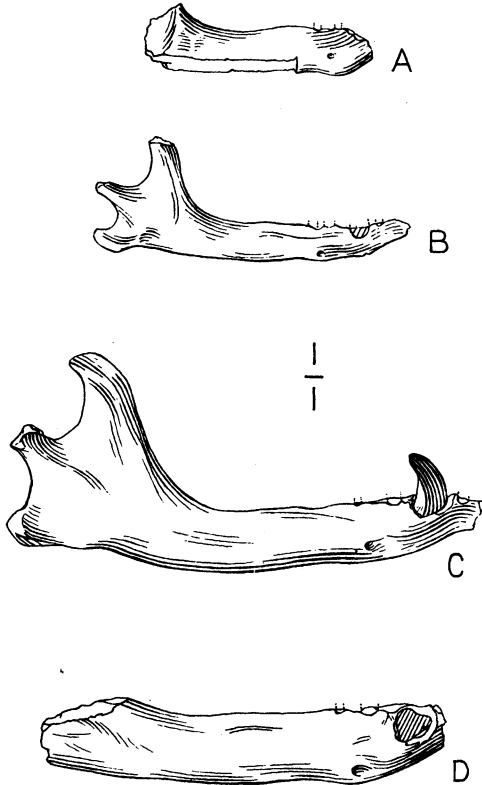
Fig. 3. *Metacheiromys*, all known species. Comparative series of external views of right lower jaws, reversed from left jaws where necessary. A, *Metacheiromys marshi* Wortman (redrawn after Wortman). B, *Metacheiromys tatusia* Osborn. C, *Metacheiromys dasypus* Osborn. D, *Metacheiromys osborni* Simpson, new species. All natural size.

Metacheiromys marshi Wortman, 1903

TYPE.—Yale Peabody Museum Cat. No. 12903. Horizontal ramus of left lower jaw and various other fragments, see below. Collected for Professor O. C. Marsh, 1873.

LECTOTYPE.—The lower jaw included in the above lot of material.

TYPE HORIZON AND LOCALITY.—Bridger Formation, Bridger Basin, Wyoming. Exact level and locality not known, but probably Bridger B at Grizzly Buttes.

REFERRED SPECIMENS.—(References partly doubtful, see below).

Amer. Mus. No. 11720; broken posterior part of right lower jaw; Bridger B2, Grizzly Buttes (Thomson, 1903).

Amer. Mus. No. 12379; parts of sacrum, lumbars, humeri, femora, tibia, pelvis; Bridger B3, Middle Cottonwood Creek (Granger, 1904).

Amer. Mus. No. 19193; hind limb bones, head of humerus, ten caudals in series, other fragments; Bridger B2 or B3, Lower Cottonwood Creek (Miller, 1922).

Yale Peabody Museum No. 13500; parts of humeri, femora, tibiæ, some vertebræ; probably Bridger C, Dry Creek (J. W. Chew, 1875).

Yale Peabody Museum No. 13502; part of pelvis, fragments of fore and hind limb bones, isolated toe bones, vertebral centra, sacrum nearly complete; Bridger B, Grizzly Buttes (1873).

Yale Peabody Museum No. 13503; parts of ilia, humerus, femur, tibia, broken vertebral centra, fragment of sacrum; Bridger B, Grizzly Buttes (1873).

DIAGNOSIS.—Edentulous part of dental border of lower jaw of about the same length as in *M. tatusia*, but teeth larger and farther apart, jaw deeper, heavier, longer. Skeleton somewhat larger, up to 15% greater linear dimensions.

The type of this species, as understood by Wortman, apparently included parts of two animals: fragments of the anterior part of the animal here recognized as *Metacheiromys marshi*, and fragments of the posterior part of the skeleton of an unidentified primate of about the same size. The latter includes proximal and distal ends of a tibia, acetabular and median parts of an ilium and some other fragments. The following of the more important items probably are correctly associated, but I take the precaution of designating the lower jaw as the lectotype:

1. Broken left lower jaw—lectotype of *Metacheiromys marshi* Wortman.
2. Both upper canines (broken) and fragment of right maxilla.
3. Other skull fragments, not characteristic as to species, including a small piece of the occiput and adjoining skull roof, broken basisphenoid, fragmentary otic bulla.
4. Centra of several cervicals and some dorsals, with many fragments of ribs.
5. Glenoid cavity of scapula, proximal and distal ends of right humerus, and most of the ulna.

It is no reflection on Wortman's known anatomical skill that he was badly misled by the few fragments of this then entirely new type of animal and by the association without duplication of parts of two different animals of the same size. The shaded parts of his drawings (Figs. 105–108; Fig. 109 is not *Metacheiromys*) are essentially correct, but the outline restorations are wrong in every case. His Fig. 105 of the right upper canine ("incisor") is slightly restored even in the shaded part— the extra-alveolar part is shown nearly twice too long and the tip somewhat too recurved. Except in size, this tooth was really almost exactly like that of *M. dasypus*, described below. It also seems probable that

enamel was absent on the internal face, as in *M. dasypus*, contrary to Wortman's statement.

The distinction of *M. tatusia* from this species is not very sharp. Osborn (1904) correctly described *M. tatusia* as smaller than *M. marshi* but gave no other explicit comparison. The differences in the lower jaws, given in the respective diagnoses, provisionally validate the species, but in the skeleton no difference has been positively established save in size, and that is vague. Amer. Mus. Nos. 12379 and 19193, and Yale Peabody Museum Nos. 13502 and 13503 are referable to *M. marshi* with little doubt, on the basis of the humeri, which vary somewhat but are all larger than in *M. tatusia* and close to the *marshi* type. Amer. Mus. No. 11720 is a lower jaw, very close to the *M. marshi* type.

Yale Peabody Museum No. 13500 is stated to be from Dry Creek, and hence (see Matthew, 1909) can hardly be from a level below Bridger C. This horizon has relatively few species in common with Bridger B. The specimen is inadequate. It is slightly smaller than the type of *M. marshi*, and the head of the humerus is distinctly narrower transversely relative to its anteroposterior length, so that it may eventually prove to be a separate species or mutation.

Metacheiromys tatusia Osborn, 1904

TYPE.—Amer. Mus. No. 11549. Incomplete skull, right lower jaw, nearly complete skeleton. Collected by Albert Thomson, 1903.

TYPE HORIZON AND LOCALITY.—Lower Bridger (B2), Grizzly Buttes, Bridger Basin, Wyoming.

REFERRED SPECIMENS.—

Amer. Mus. No. 11719: part of lower jaw, femur, ulna, and other fragments; Bridger B2, Grizzly Buttes (Granger, 1903).

Yale Peabody Museum No. 13501: right tarsus and metatarsus, broken hind limb bones, fragments of pelvis, dorsolumbar centra, last two sacrals (broken) and first seven caudals in articulation; horizon and locality unknown, possibly Bridger B at Grizzly Buttes.[1]

DIAGNOSIS.—Size small. Two lower cheek teeth equal. Lower jaw very slender, length about 42.5 mm. No sagittal crest. Skeletal processes generally less advanced than in *M. dasypus*.

Both of the referred specimens are more robust than the type, but the difference is very slight. The jaw of Amer. Mus. No. 11719 permits reasonable certainty in the reference. There are no parts in Yale Peabody Museum No. 13501 which are directly comparable with the type of *M. marshi*, but it seems closer to *M. tatusia* than to referred specimens of the larger species. It is quite possible that a large series of specimens

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[1]This valuable specimen was part of a large shipment to Professor Marsh which included material from this horizon and locality, but also some from the Upper Bridger.

would show *M. tatusia* and *M. marshi* to intergrade completely, but I believe it probable that they are distinct. The sacrum has three verte-bræ in the type of *M. tatusia,* four in a referred specimen of *M. marshi,* but this apparently great distinction I hold to be of little or no taxonomic significance; see "Anatomy-Sacrum" below.

Metacheiromys dasypus Osborn, 1904

TYPE.—Amer. Mus. No. 11718. Skull, jaws, and the pre-lumbar part of the skeleton. Collected by Walter Granger, 1903.

REFERRED SPECIMEN.—Yale Peabody Museum, Accession No. 511. A mixture of materials of several different genera, but with fragments of *M. dasypus,* including parts of astragalus, metatarsals, and phalanges. Probably from Bridger B, collected by Smith and Chew, Sept. 17, 1873.

TYPE HORIZON AND LOCALITY.—Lower Bridger (B2), Grizzly Buttes.

DIAGNOSIS.—About 75% larger than *M. tatusia.* Second lower cheek tooth minute, much smaller than first. Weak sagittal crest. Very large posterior dorsal metapophyses. Crests and processes of skeleton generally more specialized than in *M. tatusia.*

Metacheiromys osborni, new species

TYPE.—Amer. Mus. No. 12119. Horizontal ramus of right lower jaws and anterior part of left. Collected by P. Miller, 1904.

TYPE HORIZON AND LOCALITY.—Upper Bridger (D2), 75 feet above white stra-tum, Lone Tree, Henry's Fork, Bridger Basin, Wyoming.

DIAGNOSIS.—Largest known species. Lower jaw (canine to coronoid) slightly longer than in *M. dasypus* (about 10%), stouter, canine larger, bone more swollen around its alveolus.

The type of this species is the latest known metacheiromyid speci-men. It is the latest and largest known member of the suborder, but aside from its size it shows slight advance over *M. dasypus* in the known characters. The lower teeth are not more reduced.

OCCURRENCE AND ASSOCIATION

The zoning of the Bridger Formation is due in large part to the field work and study of W. D. Matthew and Walter Granger. Matthew (1909, pp. 295–307) divided the formation into five horizons, lettered A, B, C, D, and E, and each horizon into five numbered levels, as B_1, B_2, B_3, etc. The lowest horizon, A, is almost barren of fossils, as is also the highest horizon, E. In some cases it is partly possible to trace evolu-tionary advance through the levels from B_1 to B_5. For the most part, however, no faunal distinctions can be made between the numbered levels within one division of the formation. The most definite faunal break occurs between B and C. A and B constitute the Lower Bridger, the "Lower Bridger fauna" being from B, while C, D, and E form the Upper or Middle and Upper Bridger, the fauna being that of C and D.

The faunas of C and D are almost identical, although some differences have been detected and others no doubt will be established. The distinctions between B and C are due partly to evolutionary advance, few species being common to the two, but in larger part to migration and change of facies, a number of new groups appearing in C. The differences between C and D are due principally to evolutionary advance.

Thirteen specimens of *Metacheiromys* are known to me, all from the Bridger. The detailed geologic distribution is as follows:

Metacheiromys marshi
> Type (Yale Peabody Museum No. 12903)—Horizon unknown, probably Bridger B.
> Referred: Bridger B$_2$—Amer. Mus. No. 11720.
>> Bridger B$_2$ or B$_3$—Amer. Mus. No. 19193.
>> Bridger B$_3$—Amer. Mus. No. 12379.
>> Bridger B—Yale Peabody Museum No. 13502.
>>> Yale Peabody Museum No. 13503.

Metacheiromys cf. *marshi*
>> Bridger C—Yale Peabody Museum No. 13500.

Metacheiromys tatusia
> Type (Amer. Mus. No. 11549)—Bridger B$_2$.
> Referred: Bridger B$_2$—Amer. Mus. No. 11719.
>> Probably Bridger B, possibly Bridger C—Yale Peabody Museum No. 13501.

Metacheiromys dasypus
> Type (Amer. Mus. No. 11718)—Bridger B$_2$.
> Referred: Probably Bridger B—included in Yale Peabody Museum Accession 511.

Metacheiromys osborni
> Type (Amer. Mus. No. 12119)—Bridger D$_2$.

	Clark Fork	Sand Coulee	Gray Bull	Lysite	Lost Cabin	Lower Bridger	Upper Bridger
Palæanodon parvulus	+						
Palæanodon ignavus			+	?			
Palæanodonts indet.					+		
Metacheiromys marshi						+	
Metacheiromys cf. marshi							+
Metacheiromys dasypus						+	
Metacheiromys tatusia						+	
Metacheiromys osborni							+

Distribution of Palæanodonta

Metacheiromys marshi, M. tatusia, and *M. dasypus* characterize Bridger B. Bridger C contains either surviving *M. marshi* or a closely related species. From Bridger D only one specimen is known, the species *M. osborni,* being the largest of the genus and possibly a descendant of *M. dasypus.*

The beds of horizon E suggest a marked change in conditions, but no great physical distinction is noted between B, C, and D. Matthew says (1909, p. 306), "The [Green River] lake gave way to a broad flood plain on which were deposited the volcanic ash brought directly by the wind and that washed down from the slopes of the mountains to the southward, the whole being partially worked over and sorted by the streams flowing across the plain. As the deposit accumulated it banked up the streams within the basin and caused the area of deposition to extend further upstream and overlap the lower beds to the south and west. The presence of a large arboreal element in the fauna indicates that the Bridger Basin was heavily forested during the deposition of the fossiliferous beds; and the thin but extensive layers of shell-limestone that it was subject to repeated overflows which caused widespread but shallow lakes of clear water over considerable areas. Likewise we may infer from the presence of these lakes that the falls of volcanic ash were intermittent, not continuous, and from the amount of organic change in different races of animals we may infer that the accumulation of the beds was a slow process, extending over a considerable fraction of the Middle Eocene." The climate is inferred to have been warm and moist.

Horizons B and C consist chiefly of "buff and pale green tuffaceous shales and sandstones" (Sinclair, 1906, pp. 274-277, see also Johannsen, 1914), with several persistent shell limestones or marly tuffs, the "white layers" of collectors. Irrespective of horizon, much calcium carbonate is present. Shells of *Goniobasis, Paludina,* and *Unio* are abundant. "Lignitic bands . . . are frequently associated with the tuffaceous marls, registering a transition from lacustrine conditions to peat bogs." (Sinclair 1906, p. 276). Massive stream-channel lenses of coarse greenish tuffaceous sandstone are common, often with a basal conglomerate, but the bulk of the formation is of rather fine-grained material. Pure tuffs are relatively rare, and most of the sediments have been reworked by water.

The mammalian genera of the two faunas are as follows (with a few omissions of doubtfully distinct or inadequately known genera):

	B	Horizon Uncertain	C–D
MARSUPIALIA			
Didelphiidæ			
		Peratherium	
INSECTIVORA			
Nyctitheriidæ			
	Nyctitherium		*Nyctitherium*
	Entomacodon		*Entomacodon*
	Myolestes[1]		*Myolestes*
?Leptictidæ			
	Entomolestes		*Entomolestes*
	B	Uncertain	C–D
Pantolestidæ			
	Pantolestes		*Pantolestes*
Microsyopidæ			
	Microsyops		*Microsyops*
TILLODONTIA			
Tillotheriidæ			
	Trogosus		*Tillotherium*
RODENTIA			
Ischyromyidæ			
	Paramys		*Paramys*
	Mysops		
	Sciuravus		*Sciuravus*
	Tillomys		*Tillomys*
TÆNIODONTA			
Stylinodontidæ		*Stylinodon*	
PALÆANODONTA			
Metacheiromyidæ			
	Metacheiromys		*Metacheiromys*
PRIMATES			
Plesiadapidæ			
	Trogolemur		*Apatemys*
			Uintasorex
Anaptomorphidæ			
	Omomys		
	Euryacodon		
	Anaptomorphus		
	B	Uncertain	C–D
			Hemiacodon
			Uintanius
			Washakius
Adapidæ			
	Notharctus		*Notharctus*
CARNIVORA			
Miacidæ			
	Viverravus		*Viverravus*

[1]The type of *Myolestes dasypelix*, as the name implies, was found with that of *Metacheiromys dasypus*.

	B	Uncertain	C–D
	Miacis		*Miacis*
	Uintacyon		*Uintacyon*
	Oödectes		
	Vulpavus		
			Palæarctonyx
Oxyænidæ			
	Patriofelis		*Patriofelis*
	Limnocyon		*Limnocyon*
	Thinocyon		*Thinocyon*
	Machairoides		*Machairoides*
Hyænodontidæ			
	Sinopa		*Sinopa*
	Tritemnodon		
Mesonychidæ			
	Mesonyx		
	Harpagolestes		
			Synoplotherium
CONDYLARTHRA			
Hyopsodontidæ			
	Hyopsodus		*Hyopsodus*
AMBLYPODA			
Uintatheriidæ			
			Uintatherium
ARTIODACTYLA			
Dichobunidæ			
	Homacodon		*Homacodon*
	Microsus		*Microsus*
	Sarcolemur		*Sarcolemur*
	Helohyus		*Helohyus*
		Lophiohyus	
PERISSODACTYLA			
Lophiodontidæ			
	Helaletes		
Tapiridæ			
			Isectolophus
Hyrachyidæ			
	Hyrachyus		*Hyrachyus*
		Colonoceras	
		Metahyrachyus	
Hyracotheriidæ			
	Orohippus		*Orohippus*
Titanotheriidæ			
	Palæosyops		*Palæosyops*
			Telmatherium

Few additions or nominal changes have been made since 1909 when Matthew gave a complete list of species from the formation (Matthew 1909, pp. 298–302).

Following Matthew (1909, pp. 309–310), with modifications, the faunas may be roughly analyzed as to ecology:

Aërial:
>   Birds
>   Rare as fossils, probably abundant in life.

Arboreal: Largely frugivorous:
>   Primates
>   Some rodents
>   Largely insectivorous
>   Some insectivores
>   Probably some lizards
>   Carnivorous:
>   Miacidæ except *Viverravus*

The mammals largely frugivorous or insectivorous were probably very catholic in their tastes, as similar creatures are to-day. This is a large, varied, and important element of the fauna.

Terrestrial, ambulatory or cursorial:
>   Herbivorous
>   Ungulates
>   Carnivorous
>   *Viverravus*
>   *Patriofelis*
>   Hyænodontidæ
>   Mesonychidæ
>   Insectivorous
>   Some lizards

Also a large and varied part of the fauna.

Terrestrial, fossorial:
Food varied. Tillodonts and tæniodonts have gnawing anterior teeth, the latter with continuously growing, grinding cheek teeth, the former with low-crowned herbivorous to omnivorous cheek teeth. For palæanodonts see below.
>   Tillodontia
>   Tæniodonta
>   Palæanodonta

All of these animals are rare as fossils and were probably relatively rare in life.

Amphibious and Aquatic:
All zoöphagous, but probably extremely varied in diet, fish probably chiefly eating invertebrates, others mostly eating the available vertebrates, but the peculiar crocodile *Allognathosuchus* ate mollusks, and *Pantolestes* may have supplemented its diet with similar food.
>   *Pantolestes*
>   Possibly (to a less degree) some small oxyænids.
>   Crocodiles
>   Turtles
>   Fish

Amphibious mammals are rare, other amphibious animals abundant.

Relating the known biotic environment to *Metacheiromys*, none of the known fossils suggests the food of this genus, nor were any close competitors. Tæniodonts and tillodonts were much larger and with very different dental adaptations. Enemies are seen in the terrestrial carnivorous animals.

APPEARANCE AND HABITS

GENERAL PROPORTIONS

The skeletal proportions of *Metacheiromys tatusia* are in general unspecialized, resembling those of the smaller creodonts, for instance, but differing chiefly in the short neck and slightly shorter, more robust limbs. If the length of the head be taken as unity, that of the neck is about one-half, of the body nearly three, and of the tail perhaps about three and one-half along the curve. The proportions are very similar in *Tatu*, although in the latter the carapace covers what is anatomically the neck.

The trunk is well but not sharply arched, the highest point being at about the ninth to twelfth dorsolumbar vertebræ, where the height is about two-thirds of the body length from the first dorsal to the ischia. The first dorsal spines are at about the same height as those of the sacrum.

The tail was not sharply divided from the body externally, and is long, stout proximately, moderately mobile but not prehensile.

The limbs are stout, but less so than in armadillos. The disparity between fore and hind limbs is slight, the femur being one-fifth longer than the humerus. The humerus is nearly one-half longer than the radius, the femur about one-tenth longer than the tibia—proportions close to those of many primitive mammals.

The fore foot, with its large claw-cores, is four-fifths as long as the humerus. The hind foot, from the posterior end of the calcaneum, is only about a tenth shorter than the femur and about equal to the tibia in length. The claw-cores are much shorter than those of the fore foot, but this is compensated by the longer metapodials. The hind foot appears to have been normally plantigrade. The fore foot is also plantigrade, but with an ulnar rotation.

INTEGUMENT

Metacheiromys did not possess dermal ossifications. Neither of the two articulated and splendidly preserved skeletons had any such bones associated. Furthermore, collecting both in North and in South America has fully shown that in any formation containing armored edentates, the

dermal scutes are many times more abundant than any jaw or other endoskeletal remains, so that the absence of such scutes in our Lower or Middle Eocene is strong evidence of their absence in the Palæanodonta.

Osborn (1904, p. 163; 1910, p. 162) postulates a leathery shield. I believe, on the contrary, that *Metacheiromys* was covered either with horny scales or with coarse hair. The following considerations argue for the presence of horny scales:

1.   Its closest analogues and allies in the recent fauna are invariably scaled—Pholidota, Dasypoda.

2.   In recent dasypods the definite horny scales appear long before dermal ossification begins in ontogeny, and for this and other reasons it is probable that the scales are the older part of the dermal shield in phylogeny.

3.   The strong dorsolumbar metapophyses are such as might, by analogy, support either a bony or horny shield.[1]

4.   The upper surface of the cranium suggests the presence of a casque which, as it was not bony, was probably corneous.

None of these facts is conclusive, but they are very suggestive. The extent to which the scales, if present, foreshadowed the true dasypod carapace is, of course, unknown. They may more nearly have resembled those of *Manis*, but if so were probably smaller and less strongly imbricating. The tail was not enclosed in a tube as in armadillos and glyptodonts, but may well have been squamate.

Food

The chief elements in the food-obtaining apparatus of *Metacheiromys* were:

1.   A long, protrusile, prehensile tongue.
2.   Strong, cutting canines.
3.   Stout, crushing, horny cheek plates.

No other animal, fossil or recent, which possesses these characters or any nearly analogous arrangement is known.

The long protrusile tongue is inferred from the reduction of the incisors and the narrow, spout-like symphysis. Analogies are found among ungulate herbivores, which, however, have grinding teeth, but the closest resemblance is to ant-eaters, as *Myrmecophaga*, which also lack cheek teeth but are without cutting incisors or crushing plates.

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[1]They may be present without doing so in other groups, however.

The canines are large and functional and were surely essential to the animal's mode of life. They are not of laniary carnivorous type, nor are they of the offensive but not predatory type found in some herbivores. While also sharp and piercing, they show special adaptation to shearing. Although with limited enamel, they are low-crowned, are not adapted to gnawing, and are not at all analogous to the tæniodont canines. The enlarged teeth of the tree-sloths are rather distantly analogous, although not homologous, but are accompanied by large functional grinding and cutting cheek teeth. *Proteles* is similar in so far as its canines are functional and cheek teeth vestigial, but its adaptive type is clearly quite unlike that of *Metacheiromys*—normal incisors, predaceous canines, no crushing plates.

The cheek teeth of *Metacheiromys* are nearly or quite functionless, as shown by their small size, degenerate character, absence of occlusal relationships, and marked reduction from *Palæanodon* to *Metacheiromys*. They are functionally replaced by the horny plates, which were apparently lenticular in form, elongate, one in each jaw, those in the upper jaw facing somewhat outward, in the lower jaw inward. Bearing in mind the motion imposed on the jaw by the musculature, articulation, and canine occlusion, their function can have been only that of crushing.

Opposing horny plates or pads are seen in some sirenians and ground sloths, but in both cases the plates are anterior in position. In the sirenians they may accompany general reduction or complete absence of teeth, while in the ground sloths they replaced rather the incisors than the cheek teeth, which were retained and fully functional. So far as the cheek armature alone is concerned, *Ornithorhynchus* is most nearly analogous, but it is without cutting teeth and the snout is very different.

The articulation of the lower jaw in *Metacheiromys*, in keeping with the rigid canine occlusion, allows only orthal movement, with slight lateral flexibility and almost no anteroposterior movement. The well developed temporal muscles, high slender coronoid, somewhat elevated condyle, relatively posterior masseteric origin, and projecting angular process are in keeping with this orthal motion, exclude specialized predaceous or herbivorous habits, and strongly suggest the Insectivora, without absolutely disproving a diet including succulent vegetable matter.

The habitus of *Metacheiromys*, as suggested below, was fossorial, but not strictly subterranean. Its environment would probably provide any type of food available to-day in semi-tropical or warm-temperate, fairly humid regions.

These data are not conclusive, in the absence of close recent

analogues, but they seem to me strongly suggestive of a diet of partially subterranean invertebrates. The protrusile tongue would be of use in securing any small invertebrates—the adaptive type is not strictly myrmecophagous. The canines would hold and cut prey: worms, larvæ, or relatively large adult insects. The plates would crush either soft-bodied or chitinous food, perhaps also thin-shelled land mollusks. The unique combination may be an adaptation to some specific type of food which was abundant at the time but of which direct knowledge is now impossible.

LOCOMOTION AND HABITUS

The limbs of *Metacheiromys* retain some primitive features. It was quadrupedal, plantigrade to subdigitigrade (apparently with a tendency to bear more heavily on the second phalange in the fore feet and on the ends of the metatarsals in the hind), and ambulatory. The elbows were spread, and the weight rested largely on the ulnar side of the manus. It probably could not run very swiftly. Most of its specializations in the limbs are related to its partly fossorial habitus.

There are many degrees of fossorial adaptation, from an animal like a dog, which digs, but has no special modifications for this action and can hardly be called truly fossorial, to one like a mole, which finds both food and shelter underground and rarely emerges. A fairly sharp distinction may be made between animals which dig holes and burrows, but progress in much the normal terrestrial plantigrade or digitigrade manner, and those which are truly subterranean and progress through the earth as a medium somewhat as aquatic animals do through water as a medium. *Metacheiromys* clearly belongs in the former class.

Another two-fold division may be made between (1) those fossorial animals which have a broad manus with claws approximately normal and (2) those which have a narrow manus, with one or more claws very large, narrow, and long. The common mole typifies the first group, *Metacheiromys* (although not an extreme example) the second. Abel and others have suggested that the former type is an adaptation to digging in soft earth, the latter to hard earth. One may go farther, however, and correlate these differences with combinations and changes of function of importance in the phylogeny of some mammalian groups, including the edentates.

Modes of life which require great strength and rather unusual types of motion in the fore limb lead to more or less resemblance in musculature and osteology. A great many examples can be found among arboreal,

fossorial, and natatory animals. For instance, the humeri of a phalanger (arboreal marsupial), an armadillo (fossorial edentate) and an otter (natatory carnivore), while differing markedly in some respects, show special similarities surprising in three mammals which could hardly be less alike in habits and affinities. To explain such resemblances simply as convergence, although obviously correct in a strict sense, insufficiently emphasizes the fact that muscular and other anatomical adaptations to such different habits may be not merely superficially similar but actually the same to such a degree that direct change from one such specialized habitus to another may be facilitated, although apparently so improbable *a priori*.

Returning to the division of fossorial animals into broad-handed and narrow-handed with these considerations in view, each of these may show a particular ability or tendency to change of habitus. Broad-handed fossorial mammals may become natatory. The broad manus and strong pectoral musculature, developed for this type of digging, are readily adapted to swimming. *Ornithorhynchus* and *Scalopus* are the most striking cases in point.[1] Narrow-handed fossorial animals, on the other hand, may readily become arboreal. The muscular development, again, is useful in either habitat, and the claws, developed for breaking and scooping up earth, readily become organs of prehension. The relatively short-tailed species of *Manis* are fossorial and terrestrial, the long-tailed arboreal.[1] *Myrmecophaga* is fossorial and terrestrial, *Cycloturus* and *Tamandua* arboreal.[1] Some species of *Manis* (e.g., *M. javanica*), although partly aboreal, are also fossorial, and the same appears to be true of *Tamandua*. Fossorial adaptation seems to underly the whole edentate group and to have given it many of its characters. The ancestral edentates were probably fossorial to about the same degree as *Metacheiromys*. A degree of fossorial adaptation is primitive for edentates, and those which depart most widely, such as the tree-sloths, are the most specialized. Some types, such as *Chlamyphorus*, however, carried the fossorial adaptation farther than in the ancestry of the whole group.

Two types of fossorial animals may also be distinguished with regard to the motion of the arm in digging and to the frequent rotation of the hand. In one, generally more completely subterranean, such as the moles, the hand is rotated so as to rest on the radial side, the digging motion is away from the midline of the animal and the earth is pushed to each side of the body. In others, including all fossorial edentates, the hand is rotated so as to rest more on the ulnar side, the digging motion is

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[1] I believe that the fossorial adaptation was primary in these cases, but if the reverse were true the general principle of change of function between these spheres of life would not be different.

ADAPTATIONS	Metacheiromys	Tatu	Myrmecophaga	Manis	Talpa
HEAD:					
Prenasal cartilage	Unknown	Small	Small	Small	Large
Eyes reduced	Probably not	No	No	No	Yes
Macrosmatic	Yes	Yes	Yes	Yes	Yes
Ossified bulla	Yes	No (but in Dasypus, etc.)	Yes	Yes	Yes
Paroccipital processes absent	Yes	Yes	Yes	Yes	Yes
VERTEBRÆ					
Neck short	Yes	Yes	No	Yes	Yes
Some cervicals fused	No	Yes	No	No	No
Sacrals and false sacrals numerous	Four	Eight	Five	Three	Five
Tail short	No	No	No	¿No	Yes
FORE LIMB:					
Scapular spine strong	Yes	Yes	Yes	Moderately	No
Two crests on scapula	Second incipient	Yes	Yes	No	No
Clavicle present	Yes	Yes	Vestigial	No	Yes(Very short, stout)
Presternum long, crested	Yes	Yes	No	No	Very
Anterior ribs stout	Yes	Yes	Yes	No	No
Humerus short, stout	Moderately	Moderately	Moderately	Moderately	Very

ADAPTATIONS	Metacheiromys	Tatu	Myrmecophaga	Manis	Talpa
FORE LIMB:					
Muscular processes strong	Yes	Yes	Yes	Moderately	Very
Distal end expanded	Yes	Yes	Yes	Yes	Yes
Humerus horizontal	No	No	No	No	Yes
Olecranon strong	Yes	Yes	Moderately	Moderately	Yes
Larger metapodials and proximal phalanges short	Yes	Yes	Yes	Yes	Yes
a. Hand broad, shovel-like	No	No	No	No	Yes
b. Hand narrow, one to three digits enlarged, with very strong claws	Yes	Yes	Yes	Yes	No
Articulations strong, keeled	Moderately	Yes	Yes	Yes	Moderately
Manus rotated	Yes, rests more on ulnar side	No	Yes, rests more on ulnar side	No	Yes, rests on radial side
HIND LIMB:					
Ischium attached to vertebræ	By ligament	Yes, suture	Yes, suture	Ligament	Yes, suture
Pubic symphysis short	Yes	Yes	Yes	Yes	Absent
Femoral muscle attachments unusually strong	Yes	Yes	No	No	Moderately
Tibia and fibia fused	No	Yes	Yes	No	Yes
Cnemial crest strong	Moderately	Yes	Slightly	No	Moderately
Hind foot specially modified to aid in digging	No	Slightly	No	No	Yes

chiefly toward the midline of the animal, and the earth is pushed back beneath the body. *Metacheiromys* clearly dug in the latter way.

Close study of the articulation of the fore limbs shows that the hand was capable of strong supination and that it was probably habitually carried, whether in locomotion or digging, so as to bear more heavily on the ulnar side.

Some of the evidence for the fossorial habits of *Metacheiromys* and some basis for judging the degree of this adaptation are given in the accompanying table.

No one fossorial animal has all of these characters, and many of them may also occur in animals of quite different habits. Taking all of its characters together, however, there seems little doubt that *Metacheiromys* was fossorial, probably to about the same degree as *Tatu*. It certainly was not habitually natatorial, having no definite characters of this type except such as are also seen in fossorial animals. Analogy with *Manis* or *Tamandua* might suggest some climbing ability, but this I believe also to have been lacking. None of the limb or foot segments is elongated, and the claws are not as long or as curved as in most arboreal or semi-arboreal edentates. The tail apparently was not prehensile. All of its vertebræ are elongate; the articular surfaces of the centra are nearly plane, and the zygapophyses and transverse processes of the median and distal caudal vertebræ are weak or lacking.

As regards the sense organs, the brain and nasal chamber of *Palæanodon* (apparently very like *Metacheiromys* in these respects) and the cranial osteology of *Metacheiromys* itself suggest primary reliance on the sense of smell. It is markedly macrosmatic. The sense of hearing was also well developed, but vision was probably of secondary value.

ANATOMY

DENTITION

The dentition of *M. dasypus*, being most completely known, will be described, with occasional reference to other species.

There appear to have been no upper incisors. The upper canine, however, is a large and functional tooth. In lateral view it is recurved, stout, but sharply pointed. The horizontal cross section is lozenge-shaped, about twice as long as broad, the two anterior faces convex, the two posterior concave. The posterior edge is very sharp, not serrated. The anterointernal face, which wears against the lower canine, is slightly shorter (in horizontal section) and more transverse with rela-

tion to the skull than the others. The root is much longer than the crown and is strongly curved.

This tooth is followed by a diastema 6 mm. in length in *M. dasypus*, and then comes the alveolus of the sole cheek tooth. The crown is unknown, but was apparently peg-like, slightly procumbent, elliptical in section, about 1.5 mm. in longest diameter in this species. This was
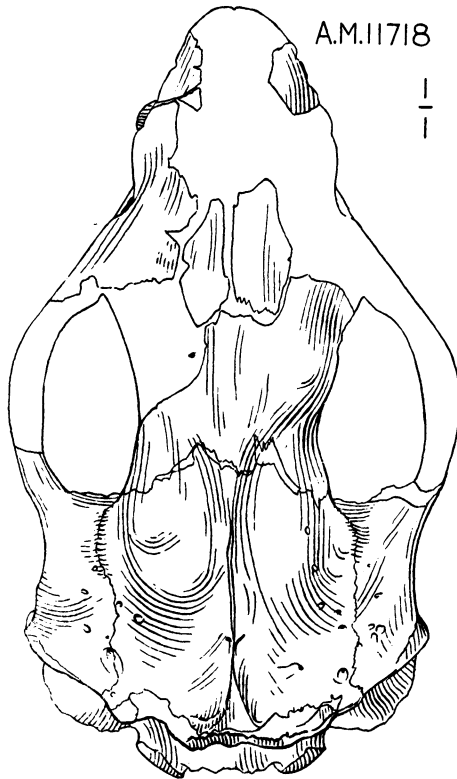

A.M.11718

Fig. 4. *Metacheiromys dasypus* Osborn. Skull of type, Amer. Mus. No. 11718. Dorsal view. Natural size.

placed at the anteroexternal margin of the horny plate, which is described in dealing with the palate, below.

The lower canine was immediately preceded by a small semi-procumbent incisor. The canine itself is large, stout, erect, recurved, almost equilaterally triangular in section. The anteroexternal face is convex, anterointernal nearly plane, posterior (which wears against the upper

canine) concave. This is followed, with short diastemata, by the two cheek teeth, known only by their alveoli which are circular and vertical. In *M. dasypus* the first alveolus is about 1.5 mm., in diameter, the second not over a third as large. In *M. tatusia* and *M. marshi* the two teeth were nearly equal in size. The anterior one passed inside the upper canine in occlusion, the posterior just behind it. Neither was near the upper cheek tooth.

The outer faces of the upper canine and the anteroexternal face of the lower are enamel-covered. The other faces appear to be without enamel in the available material.

SKULL

GENERAL ASPECT.—The skull proportions are primitive for the most part. The rostrum is neither markedly narrow nor elongate. The brain case is long, relatively low and wide, the postorbital constriction slight. The basifacial and basicranial axes are nearly parallel. The orbit is slightly in advance of the middle of the skull. The most aberrant feature in general proportions is the elongation of the basicranium posterior to the external auditory meatus, although the postglenoid part of the skull is nevertheless about half again as wide as long.

CRANIUM.—The frontals are fused in *M. dasypus*, separate in *M. tatusia*. The anterior portion is not clearly known. The postorbital prominence is very slight and rounded. The parietals, also fused in the larger species and separate in the smaller, are together nearly square. Their lateral portions bear several large vascular foramina. In *M. dasypus* there is a single low sagittal crest, while in *M. tatusia* the skull roof is smoothly rounded. The posterior suture is in advance of the lambdoid crest so that a small portion of the supraoccipital is exposed dorsally, but this does not extend forward between the parietals, and there is no trace of a separate interparietal. The dorsal part of the squamosal is nearly horizontal and forms a sloping oblong shelf on each side of the brain case proper. This part of the bone is cancellous and is pierced dorsally by several irregular foramina. The zygomatic process is slender and springs forward and slightly outward from the external side of the glenoid fossa. The latter is oval, concave anteroposteriorly, slightly broader than long, and faces forward and downward. The definite but unspecialized postglenoid process is quite separate from the ossified auditory meatus, and the otic region does not underhang the glenoid as in some armadillos. Below the end of the lambdoid crest the squamosal appears to have a process which extends for a short distance between the

tympanic and periotic toward, but not to, the stylomastoid foramen. The squamosal appears to have had little or no occipital exposure.

The occiput is especially characterized by the large triangular mastoid areas laterally. The supraoccipital has a small vertical crest and is irregularly pierced by several foramina. The foramen magnum is
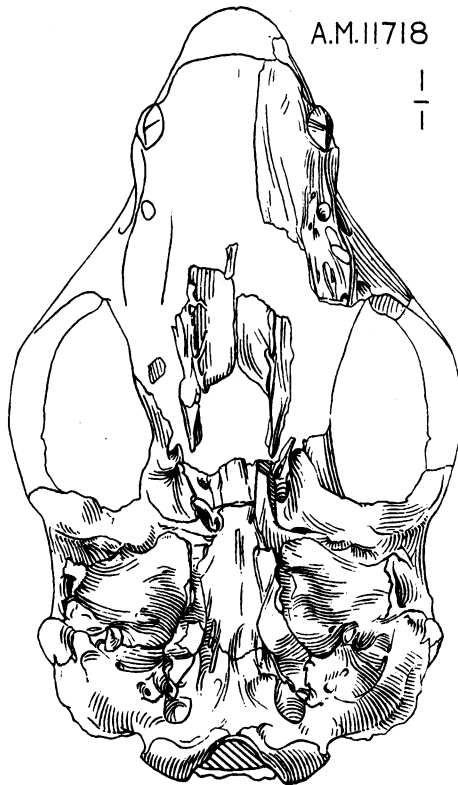

Fig. 5. *Metacheiromys dasypus* Osborn. Skull of type, Amer. Mus. No. 11718. Inferior view. Natural size.

large and elliptical. The condyles are transversely elongate, with narrow extensions of the articular surfaces extending towards the midline ventrally but not quite touching each other.

The basicranial region is marked by a relatively narrow wedge-shaped nearly flat basioccipital-basisphenoid tract and a very large and complex inflated area on each side.

There is a large ossified flask-shaped tympanic bulla and externa

auditory meatus. Separated from this bone by a definite longitudinal suture which follows a crest anteriorly and a groove posteriorly, separating its exposure from that of the basisphenoid and basioccipital, is a long, relatively narrow bone which is inflated posteriorly. This appears to be a discrete element and is probably an entotympanic. The mastoid is remarkably large, its occipital exposure nearly equaling the basal portion. It is so strongly inflated as to be almost spherical, and where it has suffered little crushing (right side of *M. dasypus* type, left side of *M. tatusia* type) no definite demarcation is seen between the basal and occipital parts.

The basioccipital-basisphenoid suture is closed, but lay between the posterior ends of the bullæ. The open basisphenoid-presphenoid contact
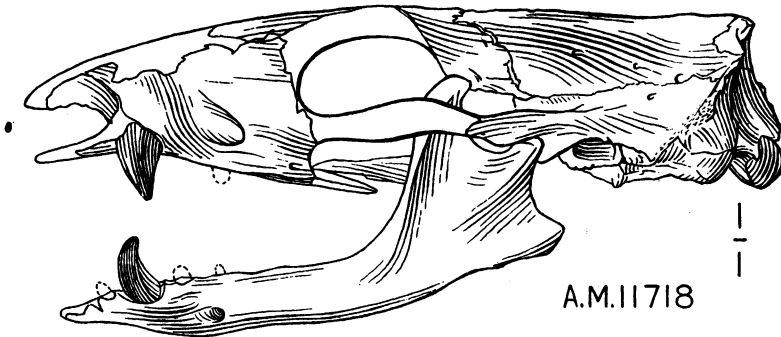

Fig. 6. *Metacheiromys dasypus* Osborn. Skull of type, Amer. Mus. No. 11718. Left lateral view. Natural size.

is between the anterior lacerate foramina. In this region there are stout alisphenoid crests, presumably crowned by or continuous anteriorly with the pterygoid crests, although the pterygoids are missing in the available material. These crests flatten out just before reaching the bullæ and are not continuous with the latter. They are not inflated.

The whole cranium is remarkable for its many foramina, the majority of which were doubtless for blood vessels. Those on the dorsal surface and occiput have already been mentioned. The condylar foramen is small but opens into a relatively large circular pit (almost exactly as in some ground sloths, e.g., *Hapalops*). The posterior lacerate foramen, immediately anteroexternal to this pit, lies between the mastoid, entotympanic, and basioccipital. There are three foramina in the mastoid near this, one anterior, one external, and one, farther away, anteroexternal to the posterior lacerate foramen. These are probably

vascular. Another lies in a groove on the more external part of the mastoid, posterior to the stylomastoid foramen. The latter is near the contact with the external auditory meatus and immediately external to the strongly marked hyoid articulation. The eustachian foramen appears to be at the anterointernal angle of the bulla (between the two tympanics
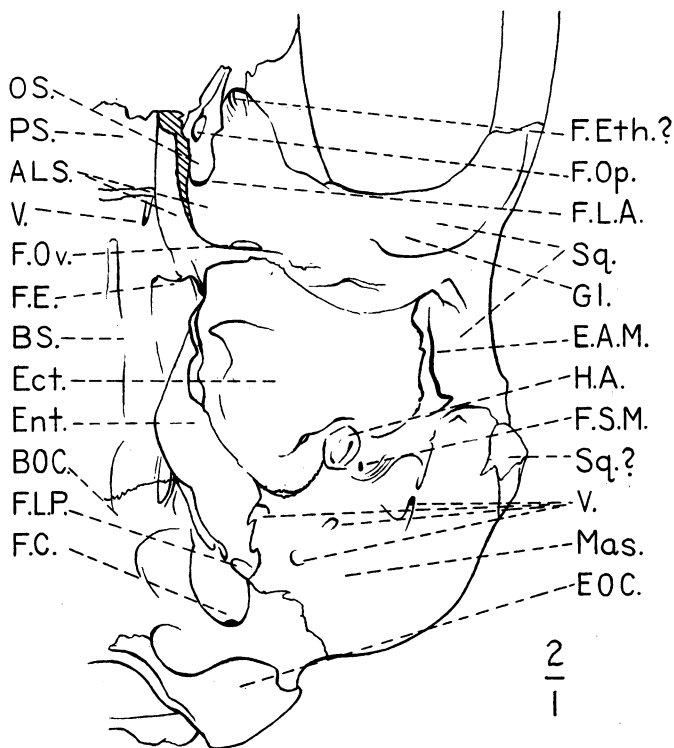

Fig. 7. *Metacheiromys dasypus* Ôsborn. Diagram of left side of base of cranium. Twice natural size.

ALS., Alisphenoid.
BOC., Basioccipital.
BS., Basisphenoid.
E.A.M., External auditory meatus.
Ect., Ectotympanic.
Ent., Entotympanic.
EOC., Exoccipital.
F.C., Condylar foramen.
F.E., Eustachian foramen.
F.Eth.?, Ethmoid foramen?
F.L.A., Anterior lacerate foramen.

F.L.P., Posterior lacerate foramen.
F.Op., Optic foramen.
F.Ov., Foramen ovale.
F.S.M., Stylomastoid foramen.
Gl., Glenoid fossa.
H.A., Hyoid articulation.
Mas., Mastoid.
OS., Orbitosphenoid.
PS., Presphenoid.
Sq., Squamosal.
V., Vascular foramina.

and the alisphenoid). The basisphenoid has a small vascular foramen on each side near its anterior end. The foramen ovale lies immediately above a buttress passing from the alisphenoid-pterygoid crest anterior to the bulla toward the glenoid process of the squamosal.

From the probable absence of a separate foramen rotundum, it would appear that the second branch of the trigeminal passed through the anterior lacerate foramen. The latter is large and is a short distance anterior to the foramen ovale and separated from it by the thin ascending process of the alisphenoid. Anterior to this is the small optic foramen, and at a greater distance anterosuperiorly is at least one small foramen (either purely vascular, or the ethmoid foramen). Except for the larger mastoid and details of the variable vascular foramina, the whole arrangement is almost exactly as in *Dasypus*.

FACE AND PALATE.—The nasals are unfused, transversely arched, and rather slender anteriorly (*M. tatusia*). They expand slightly at the tip. The lacrymal is unknown, but its facial expansion must have been small. The premaxilla is a small bone, emarginate anterolaterally, so that its facial part is crescentic. The palatal portion is unknown, but must have been markedly anterior and perhaps very small, as the palate is apparently found by the maxilla below the posterior two-thirds of the facial part of the premaxilla.

The facial part of the maxilla is of normal form. It has a well defined zygomatic process, in front of which, and well in advance of the orbit, is the large infraorbital foramen. Immediately beneath the zygomatic root is a smaller foramen opening backward.

The palate is imperfectly known and there are some anomalies which cannot be cleared up without better material. The alveolar border posterior to the canine is elevated. Immediately behind the alveolus of the single cheek tooth it becomes a broad shallow groove, with irregular longitudinal striæ and several vascular foramina. As suggested by Matthew for *Palæanodon*, this probably lodged a horny plate analogous to that of the adult *Ornithorhynchus*. It is broken off posteriorly in the one specimen which shows it (type *M. dasypus*) but judging from the position of the opposing plate of the lower jaw it must have extended back beneath the orbit for some distance. The posterior part of the palate has a broad smooth central portion flanked by elevated ridges, lateral to which are narrow irregular, longitudinally grooved areas, which seem in part to have extended above the internal part of the base for the horny plate. High palato-pterygoid crests appear lateral to the choanæ, but only their anterior ends are preserved.

MANDIBLE.—The symphysis is elongate and spout-like, somewhat resembling that of a long-jawed ground-sloth in miniature, more like that of *Myrmecophaga*. The horizontal ramus is long and slender, the mental foramen single and usually beneath the second cheek tooth. In the posterior cheek region internally there is a swelling or sloping shelf, the upper surface of which is slightly hollowed out and irregular. This probably lodged the lower horny plate.

The coronoid process is high, rather slender, and recurved. The angle extends almost straight back beneath the condyle and is of moderate size. The condyle is moderately elevated with short peduncle, the articular surface transverse.

The dental foramen is far back, beneath the posterior end of the coronoid process. As is often seen in modern Xenarthra and rarely in other groups, there are two distinct grooves on the internal surface of the
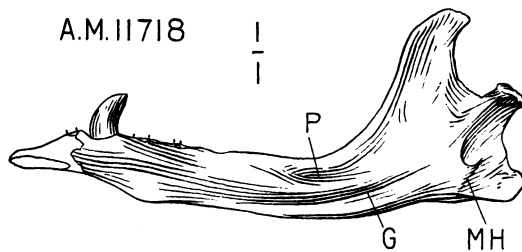

Fig. 8. *Metacheiromys dasypus* Osborn. Lower jaw of type, Amer. Mus. No. 11718. Internal view. Natural size.
G, Internal groove. MH, Mylohyoid groove. P, Hollow for horny plate.

jaw. One is broad and shallow, beginning at the posteroinferior end of the dental foramen and running downward and forward to the lower border of the jaw, probably a true mylohyoid groove. The other, generally narrow and more sharply marked, but quite variable in definition, begins anterior to the dental foramen, bends down to pass beneath the buttress for the horny plate, and then runs forward nearly horizontally until it disappears near the middle of the horizontal ramus. Bensley has adduced evidence that the similar groove of recent Xenarthra and other mammals is a vestige of the meckelian groove[1].

In general character the lower jaw is not unlike that of *Tatu* among recent edentates, but seems more primitive in the posterior part (that is,

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[1]It is here strikingly like the internal groove of Jurassic mammals, but not necessarily homologous. I have elsewhere given some evidence against considering the latter, at least, as of meckelian origin.

more like the Paleocene insectivore and creodont types) despite being more nearly edentulous.

Brain of *Palæanodon*

' It has been impossible to prepare an endocranial cast of *Meta-cheiromys*, but *Palæanodon* was apparently very similar in this respect, and a natural cast of the dorsal part of the endocranial cavity is exposed in the type of *P. ignavus* Matthew, which will be described.
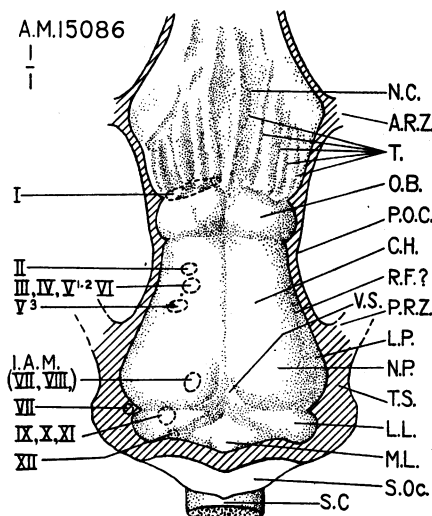

Fig. 9. *Palæanodon ignavus* Matthew.   Restoration of endocranial cast, based on skull of type, Amer. Mus. No. 15086. The skull is represented in dorsal view with the bones cut away to a horizontal plane and the endocranial cast (stippled) complete. The figure is restored and semi-diagrammatic, but shows no features not observed on one side or the other of the original.   Natural size.

I, Position of cribriform plate.

II–XII, Positions of exits of second to twelfth cranial nerves from ventral side of skull.

(VII, VIII), Point of exit of seventh and eighth cranial nerves from lower side of cerebral chamber.

A.R.Z., Anterior root of zygoma.   O.B., Olfactory bulb.
C.H., Cerebral hemisphere.   P.O.C., Postorbital constriction.
I.A.M., Internal auditory meatus.   P.R.Z., Posterior root of zygoma.
L.L., Lateral lobe of cerebellum.   R.F.?, Rhinal fissure?
L.P., Pyriform lobe.   S.C., Spinal cord.
M.L., Median lobe of cerebellum.   S.Oc., Supraoccipital.
N.C., Nasal chamber.   T., Attachments of turbinals.
N.P., Neopallium.   T.S., Squamosal table.

V.S., Venous sinus.

The length of the brain in both *Palæanodon* and *Metacheiromys* was approximately one-half that of the skull. Allowing for the part of the cerebellum concealed in this specimen by the supraoccipital, the ratio of the dorsal lengths of the olfactory bulbs, cerebral hemispheres, and cerebellum is about 5:14:6. The maximum width of the brain is about two-thirds of its length. The dorsal exposure of the olfactory bulbs is extensive, broad and short. They are on about the same level as the anterior ends of the cerebral hemispheres, which do not appear to overlap them to any great extent.

The cerebral hemispheres are, together, about one-fourth broader than long. Although the interorbital construction is slight, they are somewhat wider posteriorly. The division between the hemispheres and olfactory bulbs is definite but shallow. The division between the hemispheres (actually the impression of the frontal crest), on the contrary, is very indistinct. The cerebral surfaces are weathered, but a vague irregularity suggests the possible presence of one or a few longitudinal sulci in their upper parts. Far down on one side anteriorly is a somewhat more definite horizontal groove, probably the rhinal fissure. Below and behind this the cast is somewhat swollen (pyriform lobe).

The midbrain is not exposed dorsally. Medial and between the cerebrum and cerebellum is a deep pit, representing a strong bony projection, anterosuperior to which pass venous sinuses toward the sagittal sinus, very much as in *Tatu*, for instance. The vermis, apparently relatively broad, is thus lodged in a sharply delimited parieto-supraoccipital pit. Its transverse fissures have left no impress, as is often true. The cerebellar hemispheres or lateral lobes are large and broad. The floccular region is not exposed.

In lateral view, the brain is chiefly notable for the simple serial arrangement of its major parts. The cerebral hemispheres overlap the olfactory bulbs on the cerebellum very little, and all three segments are nearly on the same level. Both the olfactory bulbs and the cerebrum are relatively short and deep.

So far as it is known, this brain is of generally low type. In complexity the known parts stand somewhere between the simpler insectivore brains, such as that of *Ptilocercus*, and the somewhat more advanced brains of some edentates, such as *Dasypus*. Undue emphasis should not be placed on its rather generalized structure, but in proportions and some special points it is clearly very like the least aberrant recent edentate brains, and thoroughly agrees with, or even corroborates, the indications of relationships drawn from the osteological features of *Metacheiromys*.

The brain is highly macrosmatic, and may be correlated with the cast of the nasal chamber preserved in the same specimen. This nasal chamber is nearly as large as the brain itself and of similar proportions. Posteriorly there are preserved traces of five turbinals on each side in its dorsal part, and one or two shorter ones may have been present laterally.
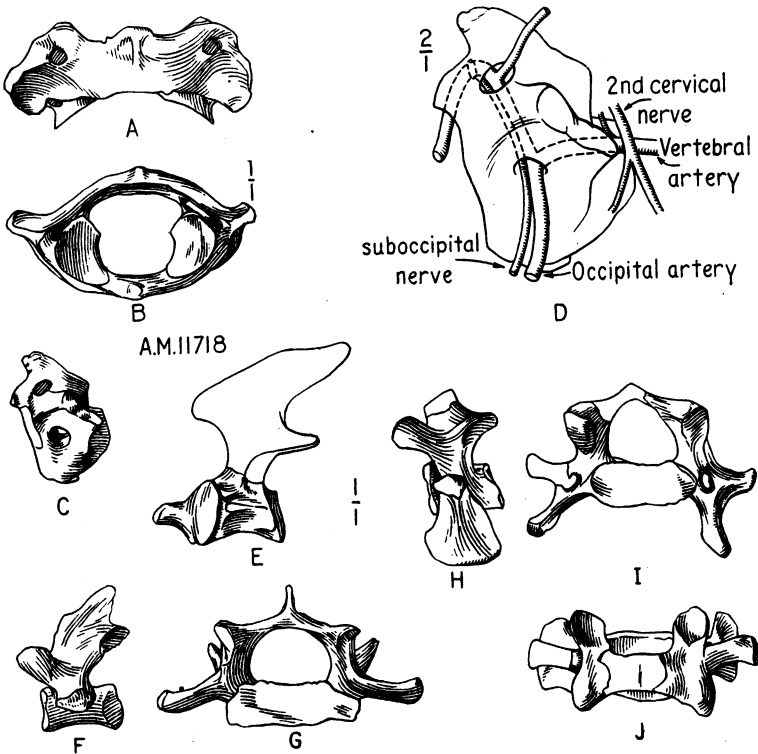

Fig. 10. *Metacheiromys dasypus* Osborn. Cervical vertebræ of type, Amer. Mus. No. 11718. A, Atlas, dorsal view. B, Atlas, caudal view. C, Atlas, left lateral view. D, Atlas, diagram of left lateral view showing positions and probable purposes of the foramina and canals. E, Axis, left lateral view, spine restored with reference to *M. tatusia.* F, Seventh cervical, left lateral view. G, Seventh cervical, posterior view. H, Sixth cervical, left lateral view. I, Sixth cervical, posterior view. J, Sixth cervical, dorsal view. All natural size except D, which is twice natural size.

VERTEBRÆ

In the mounted, associated skeleton of *Metacheiromys tatusia* there are seven cervicals, eleven dorsals, six lumbars, three sacrals and pseudo-sacrals, and about twenty-five caudals (not all of which are preserved).

This is in part anomalous, however, as one more caudal was normally fused with the sacrum, giving as probably definitive 7, 11, 6, 4, 25±.

The number of dorso-lumbars is low, but not more so than in armadillos (9–12+5–3).

CERVICALS.—The atlas is relatively slightly shorter than in *Tatu*, but is very like that of *Dasypus* both in proportions and in morphology. The articulations are monocœlous, the odontoid facet joining the narrow inferior ends of both the anterior and posterior articular surfaces. The dorsal arch is wider (anteroposteriorly) than the ventral and has a low tubercle anteriorly. The ventral arch is about as stout as the dorsal, but narrower. It is not crested, but has a small posterior tubercle. Laterally the posterior two-thirds of the vertebra bears a blunt, somewhat backwardly directed wing, its upper surface concave, its lateral edge running anterosuperior-posteroinferiorly (much as in *Dasypus*, save that here it is the lower surface which is hollowed out). The foramina and canals are as in the armadillos with one exception, which is a resemblance to *Manis:* the posterior foramina are not superomedial but superolateral to the posterior articular surfaces. A groove runs from each of these foramina upward and inward into the upper part of the vertebral canal, and another downward through a notch between the posterior articular facet and the wings.

The axis is not much like that of any recent edentate and is definitely of more primitive type. The centrum is broad, short, and low. The odontoid process is prominent, its length equal to that of the lower arch of the atlas. The superior surface is nearly flat, the lower well rounded and curving downward posteriorly. Its articular facet is continuous laterally with those of the centrum. The arch is slender, not quite as high as broad, the zygapophysial facets plane and facing slightly outward. The transverse processes (broken) were apparently simple, slender, pointing somewhat backward. The vertebrarterial canal opens anteriorly just behind the extreme lateral part of the atlantoid facet, forms a relatively large tunnel through the upper part of the base of the transverse process, and opens posteriorly outside the neural canal and superolateral to the posterior facet of the centrum. The neural spine is large, long, plate-like. An anterior projection is short but pointed; the posterior projection extends back at least over the third and possibly also the fourth cervical vertebræ.

The third cervical is imperfectly known. It had a low pointed spine, buttressing that of the axis.

The fourth to sixth cervical vertebræ are of nearly identical

pattern. The broad depressed centrum is unkeeled below and has a pair of marked foramina in the floor of the neural canal. The arch is also broad, low, slender, much as in the free cervicals of *Tatu*. The spine is broken in all the known material, but is inferred to have been low. The zygapophysial facets are inclined at about 45°, the concave anterior facets inward, convex posterior facets outward. The nearly vertical articular facet of the centrum is not, as in the free cervical vertebræ of armadillos, supplemented by separate lateral facets. At least on the fifth and sixth cervicals and possibly also on the fourth, the transverse processes consist of an upper part, the true transverse process, which is short, stout but not expanded, and projects almost straight laterally, and a separate lower part, a fused cervical rib, which is expanded antero-posteriorly and projects outward and downward. The common base of these two processes is pierced by the large short vertebrarterial canal. The spinal nerves issued freely through large notches below the zygapophyses.

The last cervical differs from the preceding ones in the absence of the separate rib process and of the vertebrarterial canal. The neural spine (preserved in *M. dasypus*) is low, sharply pointed, and inclines backward.

DORSALS.—In the complete and associated dorso-lumbar series of the *M. tatusia* type, eleven bear ribs; 1 to 5 are completely preserved in *M. dasypus* and also the broken centra of 6–8.

The first dorsal vertebra has a centrum of the same proportion and character as the seventh cervical. The capitular facet is anterior, oblique, continuous with the facet of the centrum. It is separated by a narrow groove from the concave tubercular facet, which faces forward, downward, outward, and is at the end of the stout, short, simple transverse process. The prezygapophysial facets are slightly concave and face upward and inward. The postzygapophyses have a special resemblance to those of recent edentates, particularly *Manis*, and to a less degree those of sloths and anteaters in this region. They are scale-like, separated by a notch posteriorly, their broad facets slightly concave, directed downward and slightly inward. The nerve exits are not closed foramina as in armadillos, but show an edentate-like specialization in this direction in that the posterior notch is deep and narrow, its length about half that of the centrum. The neural spine is high and stout, inclined backward, expanded distally.

Dorsals 2–8 are similar, but with progressive modifications. Unlike 1, the anterior zygapophysial facets are convex and face upward and

outward.   The neural spines are progressively longer and somewhat narrower.   The capitular facets are intervertebral and like those of the first dorsal.   The tubercular facets, concave on the first and second dorsal, are thereafter convex and their pedicles are progressively shorter.   On
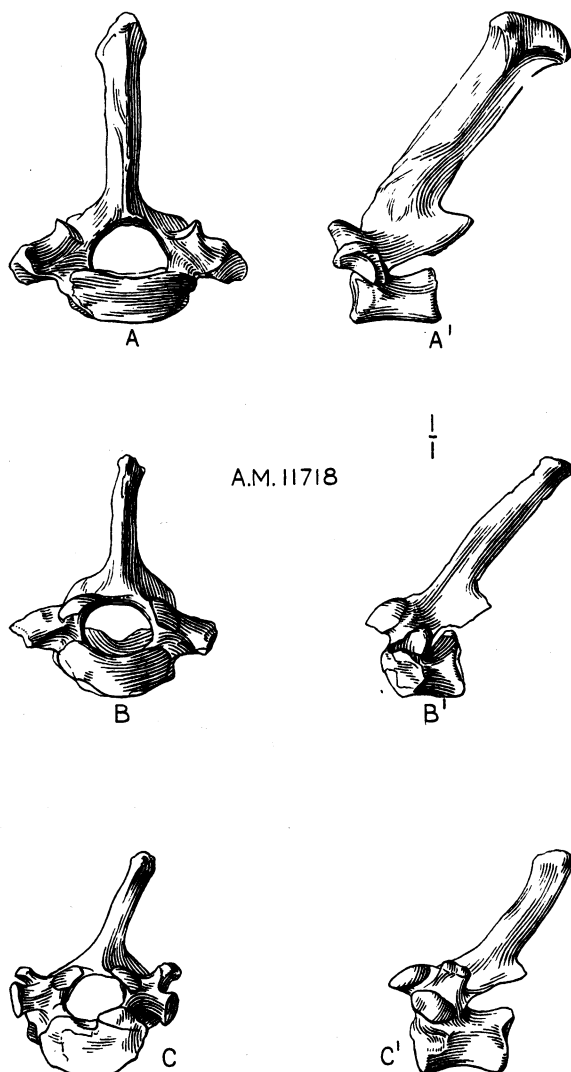

Fig. 11.   *Metacheiromys dasypus* Osborn.   Dorsal vertebræ of type, Amer. Mus. No. 11718.   Anterior and left lateral views.   A, First dorsal.   B, Second dorsal. C, Third dorsal.   All natural size.

the third dorsal a deep narrow groove appears above the tubercular facet, dividing the transverse process into a lower and an upper and slightly more posterior part, borne on the base of the arch. Subsequently these two parts become more and more separate, the upper becomes
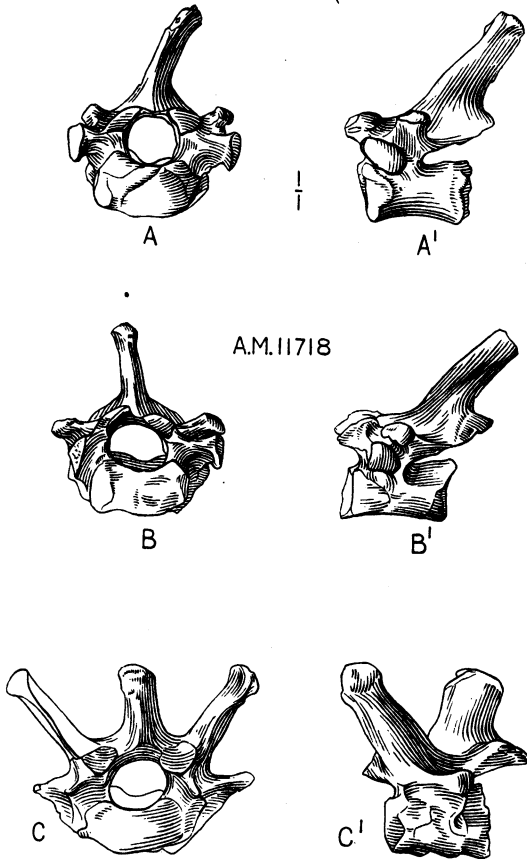

Fig. 12. *Metacheiromys dasypus* Osborn. Dorsal vertebræ of type, Amer. Mus. No. 11718. Anterior and left lateral views. A, Fourth dorsal. B, Fifth dorsal. C, Tenth or eleventh dorsal. All natural size.

longer and more posterior and assumes the position of an anapophysis.[1] Tubercular and capitular facets become progressively approximated, and are confluent on the eighth and subsequent thoracic vertebræ.

There is an abrupt change between the first eight and last three

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[1]Like many descriptive terms, "anapophysis" may include structures of quite different origin in the several orders in which it occurs.

dorsal vertebræ. The neural spines of the latter are shorter, stouter, longer anteroposteriorly, and are not directed posteriorly. The centra begin once more to become wider and stouter. The rib facets are nearly or quite confluent, the process for the tubercular facet very low and indefinite. The posterior neural notches are shorter and more open. The prezygapophysial facets (save that of d.9) are concave and face inward and upward, while the postzygapophysial facets are convex and face outward and downward. Most striking, however, is the fact that metapophyses here appear, projecting forward, outward, upward, immediately external to the prezygapophysial facets. This is weak on the ninth dorsal, and connected by an oblique crest to the anapophysis. On the tenth and eleventh this crest is absent; the anapophysis and metapophysis are larger and more widely separated. In spite of the absence of the xenarthrous articulations, there is here a special and striking resemblance to the same region in the armadillos, and as would be expected a somewhat more distant resemblance to the other Xenarthra (since they are, on the whole, more specialized or secondarily modified in the structure of the posterior dorsals and anterior lumbars). While xenarthrous articulations are not definitely incipient in *Metacheiromys*, the projection backward of the anapophysis above the nerve notch and between the metapophysis and rib facets of the succeeding vertebra forms a condition which seems to me to be an ideal point of departure for the origin of the secondary articulations and to explain the rise of the latter.

A single vertebra of *Metacheiromys dasypus*, probably the tenth or eleventh dorsal, shows that in this species the metapophyses were longer and more slender than in *M. tatusia*.[1]

LUMBARS.—The lumbar vertebræ are known only in *M. tatusia*, where they are six in number, larger than cervicals or dorsals, and increase in size slightly to the fifth. The centra are about as broad as long and are much depressed. The neural spines are progressively slightly higher to the fifth, and are erect. The zygapophyses are as in the posterior dorsals. The metapophyses are most strongly developed on the first lumbar, then decrease until on the last two or three they are hardly to be distinguished from the prezygapophyses. In the first five, the transverse processes[2] are opposite the anterior two-thirds or one-half of the centrum, and are short transversely, long anteroposteriorly. On the

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[1] The known *Palæanodon* dorsals and lumbars are broken. The metapophyses were probably smaller than in either *Metacheiromys tatsuia* or *M. dasypus*, but I believe that they were probably definitely present on the lumbar vertebra figured by Matthew (1918, Fig. 44).

[2] If serial equivalence exists, these may correspond to the "anapophyses" of the dorsals, or to the anapophyses and true transverse processes together. Morphologically, they are transverse processes.

last lumbar the transverse processes are nearly as long anteroposteriorly as the centrum, and are nearly in contact with the ilium, which they may have helped to support. On the right side the process is divided into anterior and posterior parts by a distal notch which is absent on the left side.

SACRUM.—The sacrum is completely known in *M. tatusia* and is also present, except for the neural spines and the transverse processes of the false sacrals, in a hitherto undescribed specimen referred to *M. marshi* (Yale Peabody Museum No. 13502). In *Palæanodon ignavus* there were four sacrals, the first two in contact with the ilium, the last two fused caudals, so-called false sacrals. In the type skeleton of *M. tatusia* there are but three sacrals, as noted by Osborn, the second with a weaker contact with the ilium than in *Palæanodon*, the third a false sacral. The more primitive sacrum in this animal, which is later and in all other respects more highly specialized than *Palæanodon*, is difficult to explain save as juvenile or anomalous. The epiphyses throughout the skeleton are too firmly united to permit belief that another vertebra now perfectly free would have become fused in this individual at a greater age. It is well known, however, that anomalies in the sacrum, sometimes of exactly this character, are of rather common occurrence. Fortunately the Yale specimen, No. 13502, indicates that *M. marshi*, at least, did have four fused vertebræ in the sacrum, very similar to *Palæanodon*, and it seems fully to confirm conjecture that this was definitive for the genus. It is clear that the last sacral of this specimen is homologous with the first caudal of the type of *M. tatusia*.

Viewed from above, the sacrum is roughly lyriform. The transverse processes (+ribs) of the first sacral are very stout, longer than the centrum anteroposteriorly, and firmly united by suture with the middle third of the ilia. The processes of the second sacral are narrow posteriorly but extend forward, buttressing those of the first sacral and also coming in contact with the ilia. On the third sacral the transverse processes, narrow anteriorly, are expanded and projecting posteriorly, although not in contact with the pelvis. In Amer. Mus. No. 11549 (type, *M. tatusia*) they are free, while in the more normal Yale Peabody Museum No. 13502 they are united, at least basally, with the transverse processes of the fourth sacral. Vertical foramina (each also communicating with the neural canal) pierce the bone at the bases of contiguous fused transverse processes. The centrum of the first sacral is about as broad as long and strongly compressed vertically. The succeeding sacral centra are progressively narrower and deeper.

Unlike *Palæanodon*, the zygapophyses between first and second sacrals are represented only by inconspicuous ridges on each side. Those between second and third and between third and fourth sacrals (when the latter is present) retain a more normal form, although completely fused and functionless as articulations. The neural canal narrows markedly in the sacrum. The spines are compressed transversely and form a longitudinal crest, continuous save for shallow apical notches indicating its compound origin.

CAUDALS.—In the *Metacheiromys tatusia* type, the first caudal is present, then probably two are missing, followed by eleven preserved in series and an isolated distal vertebra. There were about twenty-five in all. In Amer. Mus. No. 19193, ten caudals (probably 2–11, or 3–12) are preserved in series, and other fragments are present. In Yale Peabody Museum No. 13501, the first seven are preserved in articulation. On the first nine or ten, the zygapophyses are functional, although constantly decreasing in size, and there is an enclosed neural canal. The articulations are like those of the posterior lumbars, but narrower and with no metapophyses. The spines are low, posterior, progressively less developed, and are directed backward. On the first caudal are transverse processes, long, stout, and somewhat expanded at the ends where they are nearly in contact with the posterior ends of the ischia. On the second to seventh caudals the transverse processes are more slender, progressively shorter, directed more posteriorly. On succeeding vertebræ, probably caudals 8–10, the transverse processes are also single, progressively shorter, and directed somewhat posteriorly, but they are wider anteroposteriorly.

Posterior to about the tenth caudal, which is about the point where the zygapophyses cease to function and the neural canal disappears as such, the vertebræ are more elongate, progressively more slender, and with the processes progressively less marked. These processes here consist of two anteroposterior projections, serially homologous with the prezygapophyses; a superior median crest, ending posteriorly in a low paired projection, serially homologous with the neural spine and postzygapophyses; short anterolateral and longer posteriorly directed posterolateral projections united by lateral crests, serially homologous with the transverse processes; and a rather indefinite inferior median crest.

Chevrons, probably about 3–5, are preserved on No. 19193. The first of these is smaller, and has a more attenuated spine, directed more posteriorly, transversely bifid at the tip. The other two have in end view

nearly the shape and proportions of the latter Y. The spinous lower portion is expanded anteroposteriorly. Like the whole tail, these chevrons appear to be of somewhat more generalized type than in any recent edentate examined, although not unlike those of *Tatu*.

<div align="center">RIBS.</div>

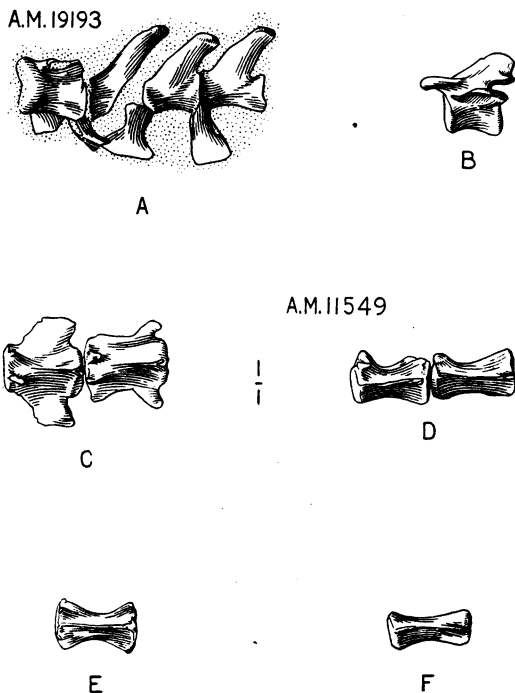There are eleven pairs of true ribs in *Metacheiromys tatusia*.

Fig. 13. *Metacheiromys*, caudal vertebræ. A, *Metacheiromys marshi*, referred specimen, Amer. Mus. No. 19193, oblique inferior view, in matrix. B-F, *Metacheiromys tatusia*, type, Amer. Mus. No. 11549. B, First true caudal, left lateral view. C, Tenth and eleventh caudals, superior view. D, Same, left lateral view. E, Isolated distal caudal, superior view. F, Same, left lateral view. All natural size.

The first rib is strikingly armadilloid. The shaft is short, very stout, expanded distally, and compressed anteroposteriorly. It is strongly curved, and the anterior thoracic aperture was wider than deep. A very short segment of cartilage intervened between the ribs and the presternum. The head and tubercle are separated by a narrow notch. The tubercular facet is directed chiefly upward and inward and is convex anteroposteriorly, slightly concave transversely.

The succeeding ribs are all more slender and are slightly compressed anteroposteriorly (not transversely as in Xenarthra). The articular facets are at first more separate than on the first rib, although they tend to merge on the more posterior ribs. Each has a very pronounced pit on the dorsal surface immediately external to the tubercle. The sixth or seventh rib was the longest, but the more posterior ones are nearly as long. Presumably the last three were floating ribs.

<div align="center">STERNUM.</div>

Five sternal segments are known in *M. dasypus*, six in *M. tatusia*. There were probably seven. The presternum is a peculiar bone, bent at an angle through the rib articulations. These are borne on
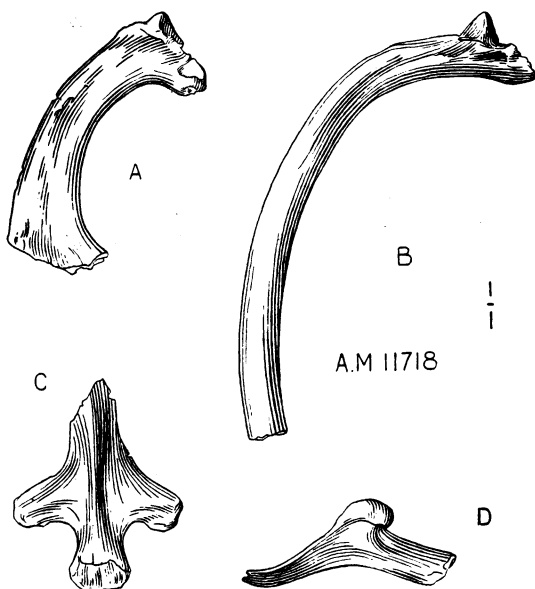

Fig. 14. *Metacheiromys dasypus* Osborn. Ribs and presternum of type, Amer. Mus. No. 11718. A, First right rib, anterior view. B, Eighth right rib, anterior view. C, Presternum, ventral view. D, Presternum, left lateral view. All natural size.

rather stout, blunt processes directed somewhat backward. Anterior to this is a long, stout plate, its superior surface concave, produced anterolaterally into the articulations for the clavicles. The part posterior to the rib articulations is shorter and stouter than that anterior. The lower surface has a prominent, sharp longitudinal crest, on each side of which it is concave. The succeeding sternal segments (except for the last which is unknown) are slightly elongate, quadrate, block-like, their free surfaces somewhat hollowed out. The sternal ribs were probably not ossified.

PECTORAL GIRDLE

SCAPULA.—The prescapular fossa is relatively narrower, the post-scapular fossa relatively broader in the scapula of *Metacheiromys tatusia* than in that of *M. dasypus*, but otherwise they are closely similar and they are strikingly like that of *Tatu*. Unlike the latter, the coracoid and suprascapular borders are primitive in character, rounded and meeting
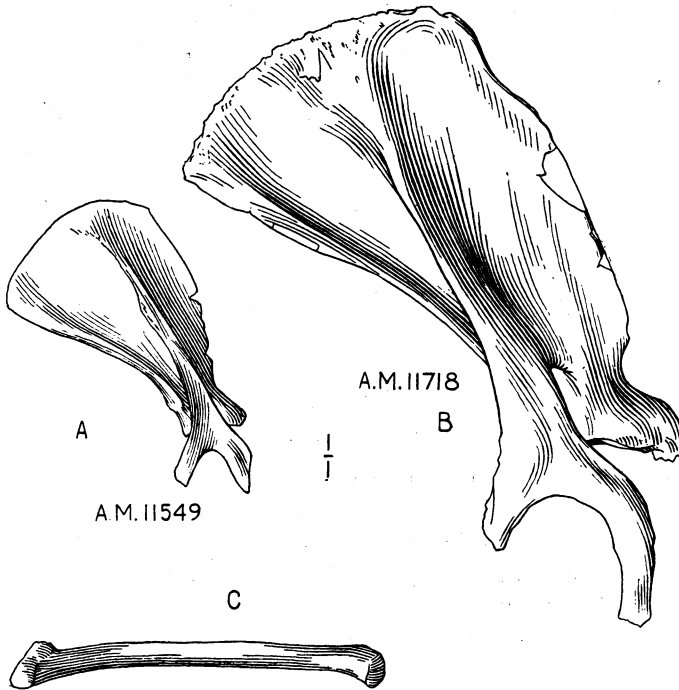

Fig. 15. *Metacheiromys.* Scapula and clavicle. A, *Metacheiromys tatusia* Osborn, right scapula of type, Amer. Mus. No. 11549, lateral view. B, *Metacheiromys dasypus* Osborn, right scapula of type, Amer. Mus. No. 11718, lateral view. C, *Metacheiromys dasypus* Osborn, right clavicle of type, Amer. Mus. No. 11718, superior view. All natural size.

at a rounded obtuse angle. The glenoid cavity is pyriform, very close to that of *Tatu* but slightly broader. The coracoid process is hook-like, large, somewhat stouter than in *Tatu* but very much less produced than in most other xenarthrans. No suture can be seen. Immediately above it is a definite notch, less marked in *M. tatusia* than in *M. dasypus*, not seen in *Tatu*, smaller and sharper than that of *Dasypus*, homologous with the coraco-scapular foramen of *Bradypus, Myrmecophaga*, etc., but not enclosed by bone.

The spine is very high, quite as much so relatively as in *Tatu*, and as in the latter it ends in an unusually strong bifid acromion. The posterior process is the smaller of the two, although relatively larger than in *Tatu*, and in the natural position of the scapula pointed downward. The anterior process, or acromion proper, is very long and curves downward, forward, and inward around the greater tuberosity of the humerus exactly as it does in typical Xenarthra. Very near the posterior border of the postscapular fossa but distinct from it, is an angulation ending below in a definite but small projection. This apparently represents an incipient secondary spine, as seen in the Xenarthra. It is more distinct than in *Bradypus*, developed almost exactly as in *Tatu keppleri*, save that, as in some ground sloths, there is no posterosuperior projection of the blade behind it.

CLAVICLE.—The clavicle is present and functional. It is a slender bone about two-thirds as long as the humerus. The lateral part is nearly straight, the medial curved upward and backward. The ends are expanded, forming stout articulations with the acromion and the presternum.

FORE LIMB

HUMERUS.—The head of the humerus is armadillo-like, oval, somewhat elongate, extending far down posteriorly, so that the humerus was directed well backward, not vertically. The greater tuberosity is very like that of *Dasypus*, while the lesser tuberosity is smaller than in that genus, intermediate between it and *Tatu*. The bicipital groove is anterointernal and is very deep and narrow, but not completely enclosed (as it occasionally is in armadillos) between the tuberosities in *M. dasypus*. In *M. tatusia* and *M. marshi* it is more open. Distally it is continued in a relatively broad and shallow groove between the internal margin of the deltoid crest and a straight internal crest which extends from the lesser tuberosity nearly to the entepicondylar foramen. The latter crest is rounded and indefinite in *M. tatusia*. In *M. dasypus* it is rounded proximally, bears a definite tubercle (for the teres major) medially, and is rather sharp, although low, distally. The deltoid crest is stouter, its distal end more overhanging in *M. dasypus* than in *M. tatusia*, but similar in general character. This crest is extraordinarily specialized, the distance from its lower end to the distal end of the humerus being less than one-third the length of the humerus (about one-half in armadillos). Its distal end is very definite and forms a prominent flange directed anterointernally. The process as a whole is broad, its surface irregularly
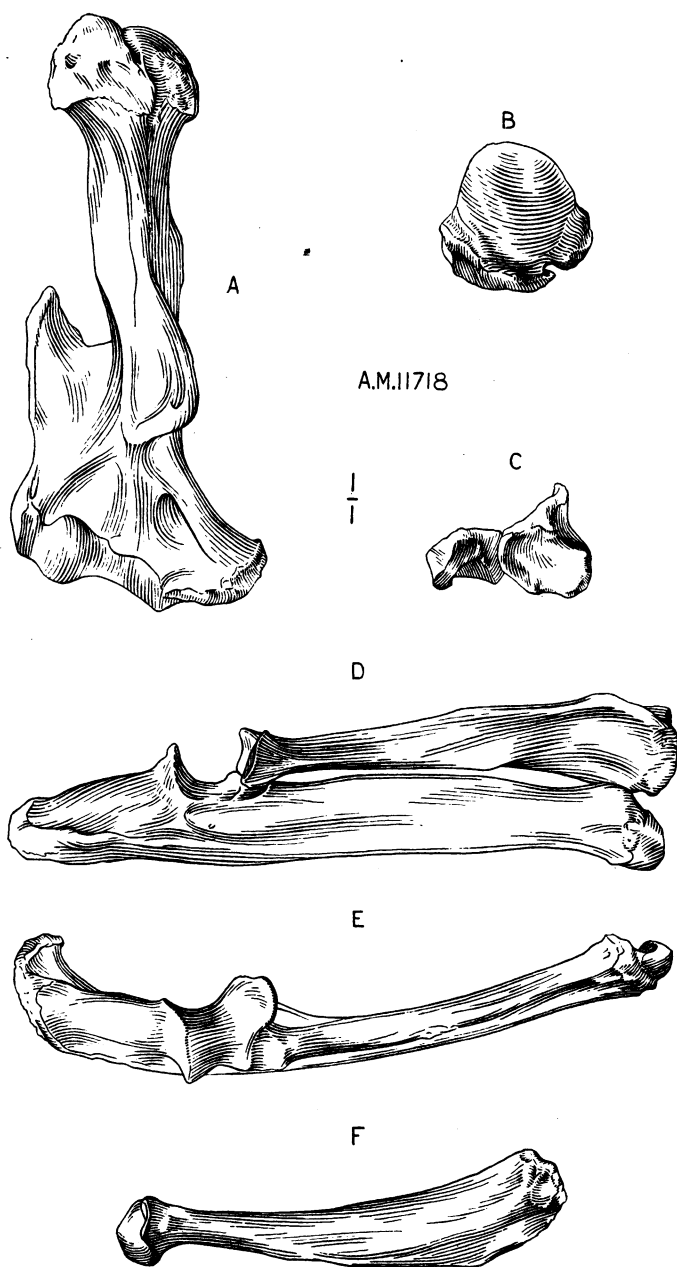
Fig. 16. *Metacheiromys dasypus* Osborn. Right fore-limb of type, Amer. Mus. No. 11718. A, Humerus, anterior view. B, Humerus, proximal end. C, Radius and ulna, distal ends. D, Radius and ulna, external view. E, Ulna, anterior view. F, Radius, anterior view. All natural size.

excavated, so that the so-called deltoid crest is represented by two distinct crests, the margins of the excavated longitudinal elevation. One runs from the most anterior part of the greater tuberosity and is continuous with the internal margin of the distal flange described above. The other crest, less definite, begins on the external face of the shaft a short distance below the external end of the greater tuberosity and converges rather irregularly toward the first crest. A transverse section through the middle part of the shaft in *M. dasypus* is almost square, the external and anterior angles formed by the two crests just mentioned, the internal angle by the teres tubercle, and the posterior angle by an inconspicuous crest which runs from just below the anterior end of the head to the notch above the supinator crest, with which it is continuous.

The deltoid process as a whole is directed more toward the entepicondyle, as in *Manis*, rather than toward the ectepicondyle as in most Xenarthra. Some of the primitive ground sloths, such as *Hapalops*, are almost intermediate in the character of the deltoid crest between typical armadillos, such as *Tatu*, and *Metacheiromys*.

The supinator crest is more highly developed than in any other mammal known to me, perhaps most nearly approached in habitus by *Phascolomys*. It is a great, flat, thin flange of bone, less curved than in armadillos, continuous distally with the ectepicondyle, ending proximally in a sharp projection (stronger in *M. dasypus* than in *M. tatusia*) separated from the shaft by a pronounced notch.

The distal end of the humerus differs chiefly from that of *Dasypus* in the more produced entepicondyle, relatively more distal and less oblique entepicondylar foramen, more spherical capitulum, small oval transversely elongate posterior fossa above the trochlea, and slightly more definite anterior fossa above the capitulum. All of these features are points of resemblance to primitive ground sloths (*Hapalops*), but the latter do not have the anterior articular groove and flange lateral to the capitulum seen in *Metacheiromys*, armadillos, *Manis* (poorly differentiated), and many other mammals.

FORE ARM.—The radius and ulna are complete, separate, about equally developed. As in the humerus, the muscle attachments are stronger in *Metacheiromys dasypus* than in *M. tatusia*. The ulna is curved, bowed outward in the same way as in the armadillos but somewhat more strongly than in *Dasypus*. It is somewhat longer and more slender than in the armadillos. The olecranon is large, about as long relatively as in *Dasypus* and similarly curved. The distal portion has a crest superomedially ending in a prominent process which projects postero-medially,

but there is no crest on the anterolateral surface as in *Palæanodon*. The semilunar notch is much as in *Dasypus* save that its superior margin (anconæal process) is more elevated and shorter transversely and that the radial facet is single and only about half as wide as the trochlear facet. Immediately below the anteromedial lip of the trochlear facet is a deep pit (insertion of the brachialis) as in armadillos. The sides of the proximal part of the ulna are excavated, the medial side about as in *Dasypus*, less than in *Palæanodon*, the lateral side about as in *Palæanodon*, less than in *Dasypus*. The shaft is compressed as in armadillos. Antero-medially it bears a crest, rugose in its middle part, the interosseous crest. A rounded crest internal to this and parallel to it defines with it a narrow anterointernal surface. The distal end suggests that of *Manis;* the Xenarthra all appear to have this part more specialized in various ways, broader in armadillos, simpler and more styliform in sloths and anteaters. The medial part ends bluntly and has no osseous articulation save for light contact with the radius. The more lateral part projects below this and has an obliquely transverse, convex facet for the cunei-form, continuous posteriorly with a smaller oval facet for the pisiform.

The radius is a stout bone. The proximal end is shorter transversely and relatively wider anteroposteriorly than in armadillos. It has two confluent articular surfaces, a cup-like capitular surface and a shelf lateral to this. In the armadillos and, less clearly, *Manis* there are three parts, a medial trochlear extension being present; in sloths and ant-eaters there is only one part (capitular). The proximal part of the shaft is flattened anterolaterally, this area being bounded by slight crests which pass (the external one rather vaguely) into the anterior crest distally. The latter crest is very strong and prominent, more so than in *Dasypus*. On the middle part of the posterolateral surface is a longitudinal rugosity, the radial interosseous crest, which in life was parallel and close to the corresponding crest on the ulna. As on the other limb bones, all of these crests are weaker and less definite in *M. tatusia* than in *M. dasypus*. The distal end is strongly expanded and heavy, larger than that of the ulna. It has a single, transverse, concave, irregular oval articular surface for the scaphoid and lunar. In *Manis* the characters of this part are similar, but the scaphoid and lunar are fused, which may indicate that the resemblance is partly convergent. In *Palæanodon* and armadillos the scaphoid and lunar facets are distinct, and in the latter there are styliform and anterior processes, absent in palæanodonts.

If the radius and ulna be articulated in a normal manner, their distal ends accommodated to the carpus, and their proximal ends to

close union with the humerus in a more or less resting position, their interosseous crests nearly parallel, and if the humerus is placed in a more or less vertical anteroposterior plane, the manus is thrown very strongly onto its ulnar side. If these articulations be maintained and the manus placed in a fully plantigrade position, the elbow is thrown far out from the body, so that the humerus must lie in an anteroposterior plane inclined at about 45°. The latter position necessitates also a strong inclination outward of the lower part of the scapula. It is probable that both positions were possible, but that the most normal and unstrained posture was between these extremes: the elbows slightly akimbo, the weight resting largely on the ulnar side of the manus.

CARPUS.—Although partly preserved, the carpus of *M. tatusia* is not readily studied. The type of *M. dasypus* includes every carpal except the trapezium on one side or both, and it will be described. The trapezium is not known in any species, except by its facets on the adjacent carpals. There are eight separate bones, only a separate centrale being lacking as it is in most mammals, even some of the most primitive, including all edentates save *Tamandua*.

The scaphoid has a proximal radial articulation, more strongly convex anteroposteriorly, posterior to which is a stout non-articular process. The dorsoventral dimension of the proximal face exceeds the tranverse width. The lunar facet is plane, and is straight proximodistal. Anteriorly it is large and ovoid, and it is prolonged posteriorly in a proximal extension, narrow by reason of emargination for the palmar part of the trapezoid facet. The palmar surface of the scaphoid is obliquely elongate transversely and consists of a central groove bordered by two projections, the external the larger. The groove may have articulated with a falciform bone, but this element is unknown. The internal side is a narrow crest between the articular facets for the radius proximally, trapezoid and trapezium distally. The free dorsal surface is relatively very small, triangular. The distal surface is the most complex. The trapezoid facet consists of a transverse, concave, more dorsal part, an oblique rounded ridge, and a smaller, less oblique palmar concavity. Internal to the latter, contiguous to the ridge and dorsal concavity but separated by a sharp angulation, is a small oval facet, slightly concave, for the trapezium. The acute angle on the dorsal half of the bone between the dorsal concavity of the trapezoid facet and the lunar facet is smooth and rounded. It came in contact along a restricted line with the magnum, but no definite surface was developed. This bone is less specialized in most particulars than in any later edentates. In *Manis* it is

fused with the lunar. In armadillos it is more transverse, with a strong magnum contact and a very oblique lunar facet. In ground sloths the magnum contact is also extensive, and may have two facets, while the trapezium facet is borne on a strongly projecting process, and *Myrmecophaga* shows the same tendency less strongly developed. Other xenarthrans are still more highly modified throughout the carpus.

The transverse width of the lunar is about equal to the proximodistal dimension, and both are considerably less than the dorsoventral depth. This bone consists of a large articular part and a smaller palmar non-articular extension. The proximal surface consists of a convex radial articulation which continues that of the scaphoid. Externally it ends in a sharp angle proximal to the cuneiform facet. It extends down on the dorsal face, narrowing to a point at the distointernal angle, leaving a triangular distoexternal non-articular dorsal surface, with a prominent vascular foramen at the extreme distoexternal angle. The external face is strongly notched, the upper part of the notch an irregular groove with several small foramina, the lower part a concave facet for the cuneiform. The distal surface has three well defined articular areas. A quadrate, concave, relatively dorsal area is separated by a sharp transverse ridge from a larger, oval, more deeply impressed, more palmar area, but both are for the magnum. External to these and in part between them and the cuneiform facet is a narrow irregular facet, directed more laterally, for the unciform. In keeping with the more serial, relatively primitive, arrangement of the carpus, the lunar has a larger magnum contact, smaller unciform contact, than in the usual xenarthran carpus. It is also relatively deeper dorsoventrally and the radial articulation extends farther down on the dorsal face. Except for the depth it is more like the lunar of *Manis*, which is, however, fused with the scaphoid.

The cuneiform is a slightly smaller bone than the two so far described and is relatively more transverse. Its proximodistal depth is slightly less than that of the lunar. Dorsal and external surfaces are irregular, non-articular, continuous with each other but sharply divided from the other surfaces. The proximal surface is chiefly occupied by a subtriangular, concave facet for the ulna. A sharp, somewhat oblique ridge divides this from the contiguous pisiform facet, which is also concave, transverse, and is inclined at about 45° to the proximodistal axis of the bone. The lunar facet is a slightly convex, oval projection on the distal half of the internal angle of the bone. The distal surface is entirely devoted to articulation with the unciform and has a more deeply impressd concave internal part and a saddle-shaped external part. It extends somewhat

farther externally than the unciform; this extension seems to be articular and it may have been in contact with the fifth metacarpal as it is in armadillos. In *Manis* they are nearly in contact. In Xenarthra other than armadillos the cuneiform is not normally in contact with the metacarpus, although in forms with a large fifth metacarpal, as most groundsloths, the approach may be very close. The extension of the fifth metacarpal lateral to the unciform, toward or to the cuneiform, was probably a character of the edentate ancestry. In *Metacheiromys* the lateral expansion of the cuneiform is less pronounced than in armadillos, however, and the ulnar facet is also less transverse and simpler.

The pisiform is strikingly armadilloid, being most identical in all its characters with that of *Dasypus*, for instance, although slightly stouter. It is L-shaped, with a basal and a projecting process at right angles. The basal process has a transverse convex facet, extending for its full length on the anterior side, which articulates with the cuneiform. On its upper surface is a concave oval facet for the ulna, which is not transverse but is confined to the external end of the basal process. The stout projecting process extends backward and downward. The internal side of the projecting process and posterior side of the basal process together form a rounded groove, the surface dense and smooth like an articular facet. This also is as in *Dasypus* and doubtless similarly marks the contact of a large falciform bone, although the bone is not present in the available material.

The trapezium is not known. The facets indicate that it was a small bone, elongate proximodistally. It apparently formed the whole carpal articulation of the first metacarpal, and may have been in contact with the second metacarpal on its external side as in *Manis* or *Myrmecophaga*. The trapezium is normally distinct but small in Xenarthra, but it seems to be fused with the trapezoid in *Dasypus*, and in the later ground-sloths it fuses with the first metacarpal.

The proximal surface of the trapezoid is triangular, the dorsal side broad but the palmar end a slender process. The whole of the more dorsal part articulates with the scaphoid, while the palmar process is wedged between the scaphoid and the magnum. The internal face has a crescentic, plane facet for the trapezium on its more volar half. A symmetrically placed and similar but smaller facet on the external side of the bone articulates with the magnum. The whole lower surface articulates with the second metacarpal. It has a dorsoventral ridge, with concavities on each side, which terminates at its palmar end in a projection fitting into a pit on the metacarpal and at its dorsal end in a

larger projection which laps down over the metacarpal. Except for this more keeled type of metacarpal articulation, the relationships of the trapezoid are normal and not unlike most edentates. In most mammals the magnum is in contact with the second metacarpal, but in the armadillos and some ground-sloths the trapezoid is in contact with the third metacarpal. The former is clearly the primitive condition, and is re- tained in *Manis* and in *Myrmecophaga*. In some ground-sloths, e.g., *Hapalops, Mylodon,* there is no distinct overlapping here visible in the dorsal aspect, the condition being as in *Metacheiromys*. In other ground- sloths, e.g., *Megalonyx, Nothrotherium,* the trapezoid articulates with the third metacarpal as in armadillos.

The magnum is of about the same size as the trapezoid and cunei- form, not reduced as in armadillos. As already described in dealing with that bone, it articulates proximally with the lunar. The internal side has two rounded facets, one convex, relatively dorsal, facing some- what proximally, for the trapezoid, the other concave, larger, more palmar in position, facing somewhat distally, for the palmar proximo- external projection of the second metacarpal. The external side of the magnum has an irregular median excavation for contact with the unci- form. The distal end articulates with the third metacarpal in nearly the same way as does the trapezoid with the second metacarpal. Here, however, it does not constitute the entire dorsal part of the metacarpal articulation, the unciform overlapping this metacarpal externally as it does in most mammals, including all edentates.

The unciform has a globular proximointernal process which articu- lates with the cuneiform save for a posterior facet for the lunar. A shelf external to this globular prominence is also for the cuneiform. The internal surface has a large facet for the third metacarpal, with a median promi- nence which fits into a corresponding notch on the latter. The distal surface has the articulation for the fourth metacarpal, which, unlike those for the second and third, is transversely elongate, unheeled, strongly concave dorsoventrally. Lateral to this but continuous with it is a small area for the fifth metacarpal. When the bones are articulated, this passes evenly into the lateral area of the distal surface of the cuneiform, already mentioned as probably helping to carry the fifth metacarpal.

METACARPALS.—Only three metacarpals are represented by bones in present collections, but there certainly were five digits in the manus of *Metacheiromys*. Of these metacarpals, III is stouter and longer than II or IV. The latter are nearly equal, but II is slightly stouter and longer. The lengths of I and V are unknown, but V may have been

slightly stouter than I, and both were more slender than II, III, or IV. Their carpal contacts, already discussed, may be given in résumé:

    I.—Trapezium only.
    II.—Chiefly trapezoid, with a small magnum articulation near the palmar side.
    III.—Chiefly magnum, but with a fairly large, strongly oblique unciform articulation.
    IV.—Unciform only.
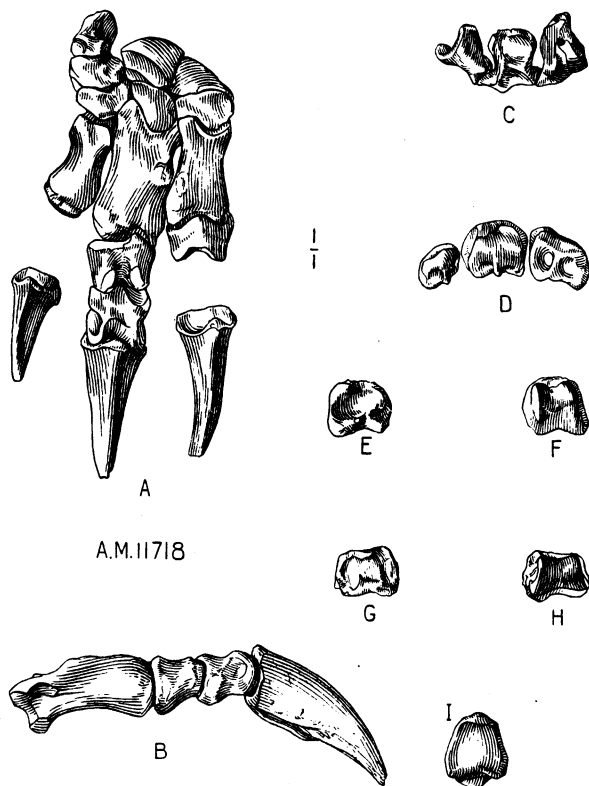   V.—Unciform and cuneiform.

Fig. 17. *Metacheiromys dasypus* Osborn. Right manus of type, Amer. Mus. No. 11718, A, Manus, dorsal view, partly restored from other side, wholly missing parts omitted. B, Third metacarpal and digit, external view. C, Second to fourth metacarpals, proximal view. D, Second to fourth metacarpals, distal view. E–F, First phalanx of third digit, proximal and distal views. G–H, Second phalanx of third digit, proximal and distal views. I, Terminal phalanx of third digit, proximal view. All natural size.

They also articulate with each other proximally, except that, as in all edentates which possess this digit, the first was probably free, the internal facet on the second probably being for the trapezium.

In proximal aspect the base of metacarpal II is quadrate, elongate dorsoventrally. The base (as also on III and IV) extends well below the shaft ventrally. It is broadly emarginate laterally, distinctly notched on its palmar edge. The shaft is short, stout, slightly arched, irregularly triangular in section. On its dorsoexternal border distally is a rough prominence for part of the extensor carpi radialis insertion. On the external surface at the proximal end are two separate facets for metacarpal III. On the internal surface at the proximodorsal angle is a single small facet, presumably for the trapezium. The head is wider than the proximal end. Its articular surface will be described below.

The proximal end of metacarpal III is not notched ventrally, but both lateral sides are deeply notched and the bone expanded dorsal to these notches. The shaft is longer, more arched than that of II, the extensor carpi radialis tubercle larger, and in the middle of the dorso-internal edge. The expansion of proximal and distal ends is about equal.

Metacarpal IV is a smaller, more slender bone than either II or III, its ends wider transversely than deep, the shaft not distinctly arched and somewhat compressed dorsoventrally.

PHALANGES.—The phalangeal articulations show modifications specifically armadilloid but such as could theoretically give rise to any edentate characters in these parts.

The distal articulation of the three median metapodials has a short sharp keel flanked by two pits ventrally, while the dorsal part is transversely cylindrical. The proximal end of the first phalanx, conversely, has a broad transverse groove dorsally and a notch flanked by two projections ventrally. The distal articulation consists of a broad dorsoventral groove with high lateral ridges and with an inconspicuous median tubercle at the palmar end of the groove. The proximal end of the second phalanx has two lateral dorsoventral grooves and a median ridge, projecting in a point dorsally, bifurcating and enclosing a small pit ventrally. The distal articulation is a simple broad dorsoventral groove. In the usual armadillo manus, the distal articulation of the median metacarpals consists of a broad dorsoventral groove with a median keel sharper ventrally. That of the first phalanx is a similar groove but with the keel represented only by a tubercle at the ventral end, more definite than in *Metacheiromys*. The distal end of the second phalanx has a broad simple groove like that of *Metacheiromys*. In *Manis* and the

Miocene ground sloths, the first articulation has a sharp, high, complete dorsoventral keel, the second a simple narrow groove, the third a similar groove but longer (more nearly forming a complete circle), very pulley-like. Other Xenarthra are in various ways still farther removed from the relatively primitive conditions in *Metacheiromys*.

The phalanges are all unfused, the first and second phalanges of about equal length. These phalanges are short and stout, but the first are not so much reduced as in the median toes of most Xenarthra.

Although the other phalanges of these toes are of nearly the same size, the claw-core of the second digit is about 50% larger than that of the fourth. That of the third is largest of all. These terminal phalanges resemble those of the Miocene ground-sloths very closely. Compared with *Hapalops*, they are somewhat longer relative to their height, the proximal ends are less compressed, the dorsal process weaker, the median articular keel lower and more rounded. The vascular foramina and impressions are closely similar. Hoods are not preserved, but small ones may have been present. The claw-cores of the second and third digits have very small distal fissures, much as in *Hapalops;* that of the fourth does not.

PELIS

The pelvis is almost completely known in *M. tatusia*, and there are various broken parts referred to *M. marshi*. Except for the distal end of the left femur, none of the posterior part of *M. dasypus* is yet known. Unless otherwise specified the description from this point is based on *M. tatusia*. These parts are fairly well known in *Palæanodon* and have been thoroughly described by Matthew (1918), with brief reference to *Metacheiromys*.

The ilium is a long bone, little expanded anteriorly. The anterior end extends well beyond the sacral joint and is everted about as in *Dasypus* (in which, however, the free projection is relatively shorter). The distal margin is thickened, but less so than in the armadillos. The lateral crest is vague and rounded anteriorly, but sharp and prominent on the middle and posterior part of the ilium. It divides the lateral face of the bone into two subequal areas, an upper, somewhat concave area, nearly horizontal posteriorly but vertical anteriorly, and a lower, more nearly plane area. The upper surface widens slightly anteriorly, the lower narrows.

The axis of the ischium continues that of the ilium, which is at a very small angle with the sacral axis. The ischium has a sharp supero-

medial crest which is nearly in contact with the transverse processes of the last two sacral and first caudal vertebræ (in the *M. tatusia* type, last sacral and first two caudals).   In all Xenarthra this contact is complete and a varying number of caudals is added to the sacral complex.   In *Manis* there is a ligamentous union between the posterosuperior spine of the ischium and the last sacral.   In *Metacheiromys*, however, although
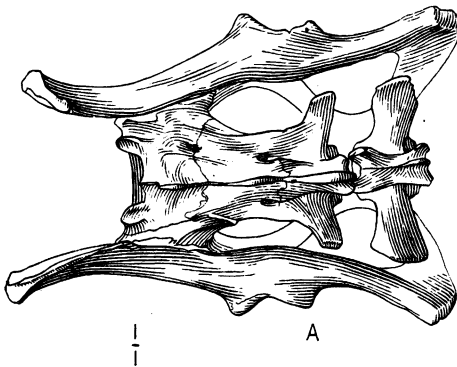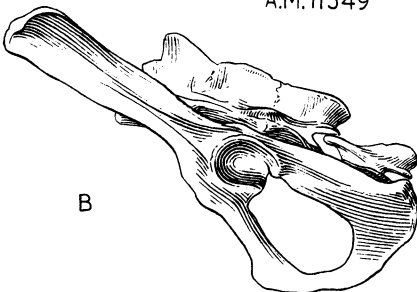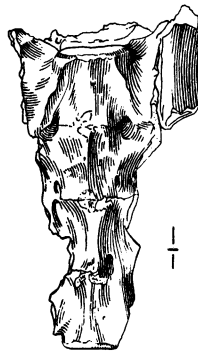

Y.P.M. 13502
Fig. 19

A.M. 11549

Fig. 18.   *Metacheiromys tatusia* Osborn.   Sacrum and pelvis of type, Amer. Mus. No. 11549.   A, Dorsal view. B, Left lateral view. Natural size.

Fig. 19.   *Metacheiromys marshi* Wortman. Sacrum of referred specimen, Yale Peabody Museum No. 13502.   Ventral view.   Natural size.

Fig. 18

the union may have been like that of *Manis*, the ischium on the whole is more Xenarthra-like in spite of its relatively primitive character.   Its posterosuperior angle is everted, and from it runs forward a crest, sharp posteriorly, which separates a narrow upper area from a larger lower area.   The latter is a flat, spatulate expansion of the ischium, continuous below and anteriorly with the post-obturator bar.

      The acetabulum is very like that of *Hapalops*. The posterior extension of the articular surface is narrower than in *Tatu*, the upper rim less emarginate than in *Dasypus*.

As Matthew has pointed out, the pubis is thoroughly xenarthran in character. It arises beneath the anterior part of the acetabulum, and is a slender bar directed strongly downward. The obturator foramen is very large, the pubic symphysis short, apparently very little longer than in *Dasypus*. The pelvic aperture is broad and shallow.

HIND LIMB

FEMUR.—As pointed out by Matthew, the *Metacheiromys* femur is like that of *Palæanodon* save for its greater compression anteroposteriorly, broader and shorter trochlea, and some variable minor details. The third trochanter, however, is not higher up the shaft, but, taking averages for both genera, almost exactly in the same position. The head is hemispherical, the fovea large, deep, posterointernal, almost notching the border of the articular surface. The head is nearly sessile, the articular surface (as in all edentates) extending down to the lowest level of the notch between the head and greater trochanter. This trochanter is stout and projects about as far above the notch as does the head. Its development is much as in gravigrades, in which, however, the notch is not so deep. The digital fossa is also gravigrade-like, deeply impressed, vertically elongate, in the posterointernal part of the greater trochanter. The lesser trochanter is below the head, projecting posteriorly and slightly internally. This is its primitive placental position, least modified in the armadillos among later edentates. The intertrochanteric crest is also armadilloid—broad, rounded, very indefinite. It is wholly absent in the sloths and in *Manis*. In *Palæanodon* it is more distinct than in *Metacheiromys*. The shaft of the femur is flattened anteroposteriorly, rather more than in *Dasypus* or *Tatu*, less than in gravigrades or *Manis*. Its curvature is about as in *Tatu*, less bowed outward than in *Dasypus*. The third trochanter is slightly above the middle of the shaft. It is gravigrade-like, weaker than in armadillos, and not, as in these, notched above. A crest runs upward and slightly backward from it to the base of the greater trochanter, another distally to the lateral epicondyle, but the latter crest is rounded and less definite than in the terrestrial Xenarthra. The latter have a sharp, more or less expanded crest above the lateral epicondyle and sometimes (e.g., *Xenurus*) a smaller one above the medial epicondyle, neither of which is definitely developed in *Metacheiromys* although the lateral crest is incipient.

As in *Manis* the popliteal surface is plane, but there is a shallow depression anteriorly above the patellar groove. The distal end of the femur is almost exactly like that of *Dasypus* and also very similar to that

of *Manis* save for the narrower patellar groove. The medial condyle projects farther posteriorly than the lateral condyle, but the disparity is less marked than in some Xenarthra, such as *Hapalops*. The distal end in *M. tatusia* is from a third to a half wider than deep (anteroposteriorly). In *M. dasypus* it is less compressed anteroposteriorly and the depression above the patellar groove is less pronounced. The patellar and condylar articular surfaces are continuous.
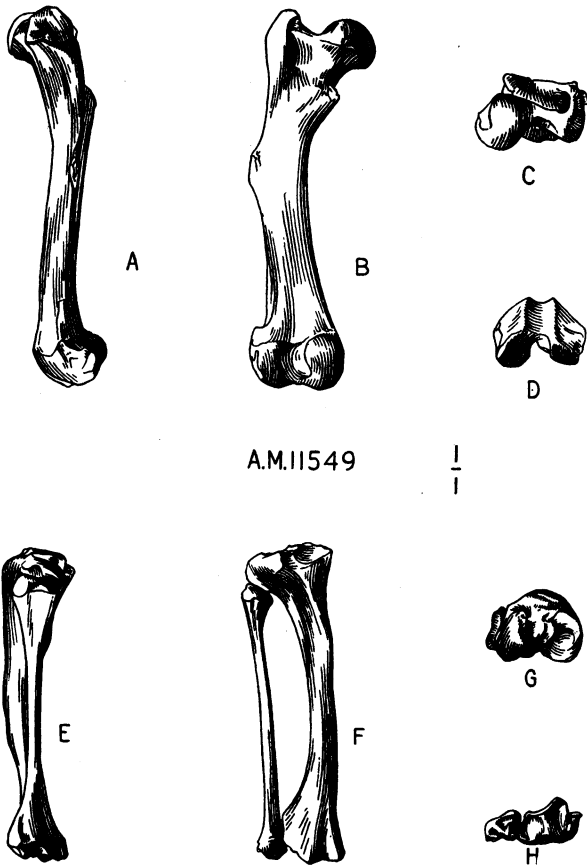

A.M.11549

Fig. 20. *Metacheiromys tatusia* Osborn. Left hind limb of type, Amer. Mus. No. 11549. A, Femur, lateral view. B, Femur, posterior view. C, Femur, proximal view. D, Femur, distal view. E, Tibia and fibula, lateral view. F, Tibia and fibula, posterior view. G, Tibia and fibula, proximal view. H, Tibia and fibula, distal view. All natural size.

Viewing the femur as a whole, it is almost ideally of generalized xenarthran type. In most of its characters it is closest to the primitive gravigrade femur, as in *Hapalops*, but the anteroposterior compression is less and some accompanying specializations, such as the absence of the intertrochanteric ridge and more internal lesser trochanter, are also less developed, although indicated. It shares some peculiarities, apparently primitive, with armadillos, but lacks their particular specializations, such as the extraordinary development of the greater and third trochanters and the broad, open, indefinite digital fossa. *Myrmecophaga* has a very aberrant femur, the greater trochanter small, digital fossa absent, lesser and third trochanters merely vague rugose swellings. *Manis* and the tree sloths have curiously convergent types of femora, which must have been independently derived from something more like *Metacheiromys*. In both, the head has no fovea, the greater trochanter is relatively small and low, there is no digital fossa or intertrochanteric ridge, the lesser trochanter is wholly internal (probably its most primitive position, but certainly secondary in these cases), the shaft is straight and flattened, and the third trochanter is absent. Nothing very like this type of femur occurs in any other animals, so far as I am aware, and its independent development in these very distantly related edentates is noteworthy.

The patella is known in Amer. Mus. No. 19193, referred to *M. marshi*. It is a small, thin, lenticular bone, irregularly elliptical, with no special peculiarities.

CRUS.—Tibia and fibula are complete and separate. In the type of *M. tatusia* the distal union is not sutural as it is in all Xenarthra and as it appears to have been in *Palæanodon*. The difference between *Palæanodon* and *Metacheiromys*, however, is really slight, and closer union may have occurred in the latter in older individuals or other species.

The tibia is arched forward about as in *Dasypus*. The proximal end resembles that of *Dasypus*, save that it is more transverse, the medial condyloid surface concave and rising to a sharp prominence externally, and the anterior tuberosity less prominent. The large, smooth, oblique fibular facet lies under the posteroexternal part of the lateral condyle. The upper part of the shaft is triangular in section, with a large convex internal face, smaller concave external face, and still smaller and more concave posterior surface. In armadillos the first two surfaces are larger and the last smaller, but the structure is similar. The cnemial crest, which separates the external and internal surfaces, is strong, but less so than in armadillos. The medial margin proximally forms a distinct,

thickened, rugose crest. The interosseous crest is not so sharp and dis-
tinct for the whole length of the bone as in armadillos. Its proximal and
distal parts are prominent and the latter is sharp, but the median part is
more indefinite.

The distal fibular articulation is a small triangular vertical facet at
the end of the interosseous crest. Aside from this the distal end is
similar to that of *Dasypus* except that in the latter the malleolar sulcus
is double, in *Metacheiromys* single and slightly more anterointernal.
The internal malleolus is less produced than in *Manis* and, of course,
much less than in the primate tibia wrongly referred to *Metacheiromys
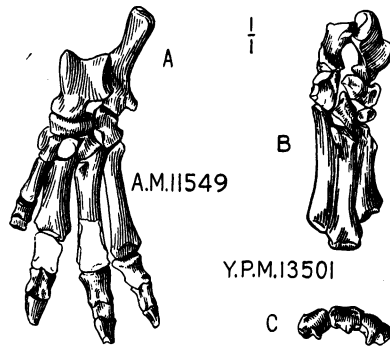marshi* by Wortman.

Fig. 21. *Metacheiromys tatusia* Osborn. Pes. A, Left pes of type, Amer. Mus.
No. 11549, dorsal view, fifth digit (not preserved in any specimen) omitted. B, Right
tarsus and metatarsus of referred specimen, Yale Peabody Museum No. 13501,
dorsal view as preserved, somewhat distorted. C, Same, distal ends of three middle
metatarsals. All natural size.

The fibula is a slender, straight rod much like that of *Manis*, less
curved and crested than in most xenarthrans. The head is expanded
anteroposteriorly, but the median and distal parts of the shaft are cylin-
drical. The interosseous crest is distinct on the distal half of the bone,
but it is small. The lateral malleolus has a distinct process projecting
straight laterally, as in *Manis* but stronger. The astragalar facet is
similar in shape to that of the armadillos, longer, narrower, more oblique,
and at a more open angle to that of the tibia than in *Manis*. The latter
genus is peculiar in having the fibula in contact with the calcaneum by a
facet immediately posterior to that for the astragalus and nearly at right
angles to it. This is not present in the Xenarthra or Palæanodonta.

TARSUS.—Most of the foot bones are present in the type of *M. tatusia,* but only their dorsal surfaces can be studied, as it is inadvisable to remove them from the base in which they were mounted twenty-five years ago. In Yale Peabody Museum No. 13501, doubtfully referred to *M. tatusia,* the right tarsus is complete, except the tuber calcis and the entocuneiform, and the three median metatarsals are present, all in articulation but free of matrix. In Amer. Mus. No. 19193 some isolated tarsals and toe bones are present.

Matthew (especially 1909) has emphasized the value of the astragalus in ordinal classification, and the same authority (1918) has pointed out that the astragalus of *Palæanodon* shows resemblances to the Insectivora on the one hand, Xenarthra on the other. It is rather difficult to designate a general xenarthran type of astragalus, for in the ground-sloths and tree-sloths this bone has extreme divergent specializations. There is, however, every reason to believe that these arose from the type more nearly preserved in ant-eaters and armadillos, a relatively slight modification of the insectivore astragalus. This primitive type of xenarthran astragalus has the following chief characters:

> Body relatively broad and short.
> Astragalar foramen absent.
> Groove of trochlea broad, deep, oblique, its lowest part relatively internal.
> Crests high, sharp; the external crest higher, sharper, and longer.
> Malleolar facets nearly vertical.
> Neck distinct, constricted, but short.
> Articular surface of head convex from side to side and extending up almost to the body of the astragalus internally.

The astragalus of *Palæanodon* is much like this, but shows distinctions, all of which approach the most generalized insectivore type and must be considered as primitive. The body is relatively narrower and longer. The trochlea is less oblique, bottom of groove more central, keels more equal. The neck is slightly longer and more slender. In *Metacheiromys* there is definite advance in the direction of the Xenarthra. The body is relatively wider, and the trochlea is asymmetrical in the xenarthran way.

As Matthew has pointed out, the astragalus is more specialized in *Manis* than in the armadillos, although *Manis* is, on the whole, the less advanced type of the two. The trochlea is relatively longer, triangular, the groove obsolescent. The head has a facet for the navicular which

is concave externally, convex internally (cf. *Myrmecophaga*), and it also has a cuboid facet.   All of these peculiarities are paralleled in the ground-sloths.   They do not involve such great differences from the dasypod type as might at first sight appear, and could be derived quite readily from the *Metacheiromys* type of astragalus.

The calcaneum is like that of *Palæanodon* except that it is a little shorter and stouter and that the peroneal tubercle is much more prominent—both points of resemblance to armadillos.

The navicular is relatively deeper proximodistally than in *Palæanodon* and the proximal projection from its ventrointernal angle is less pronounced, although, as in the armadillos, it projects backward along the head of the astragalus almost to the body of that bone.   On its lower surface it has a convex facet which probably was in contact with a sesamoid, as in armadillos or *Manis*.   The external surface of the navicular has a vertical, dorsoventrally convex cuboid facet.   The distal surface has externally a concave ectocuneiform facet, which is oblique and faces somewhat outward.   It is relatively narrower than in *Dasypus*.   The mesocuneiform facet is relatively larger than in *Dasypus*, but, as in that genus, deeper than wide.   It is convex dorsoventrally, somewhat concave transversely.   The entocuneiform facet is similar to that of *Dasypus*, deep, narrow dorsally, wider ventrally, strongly convex dorsoventrally.

The cuboid is relatively longer proximodistally than in *Dasypus*. The facet for the calcaneum is long, convex.   The cuboid does not, as in *Manis* and ground-sloths, come in contact with the astragalus.   Along its dorsal edge, at least, the internal face has a proximal facet, chiefly for the navicular but with some contact with the ectocuneiform, and a separate distal facet for the ectocuneiform.   Ventrally there is a median projection (much as in *Manis* but larger) immediately proximal to a rounded transverse groove.   The distal surface has a large, concave, oblique facet, facing somewhat outwardly, for the fourth metatarsal, and a very small, triangular, convex, more plantar facet for the fifth metatarsal.

Ento- and mesocuneiforms are very *Dasypus*-like, and have the same articulations—the entocuneiform with the navicular proximally, with the mesocuneiform and (by a large strong facet) second metatarsal externally, and with the first metatarsal, which it overlaps as in *Dasypus*, distally; the mesocuneiform (smallest bone of the tarsus) with the navicular, ectocuneiform, second metatarsal, and entocuneiform in the almost universal way.

The ectocuneiform (exposed only on the dorsal side in available material) is not very unlike *Dasypus*, but differs superficially in having the distal end wider than the proximal and both strongly oblique, more proximal externally. As in armadillos, it articulates solely with the third metatarsal distally and forms nearly the whole proximal articulation of that bone. A large sesamoid (preserved in Yale Peabody Museum No. 13501) occurs on the plantar side of the tarsus between the ventral processes of the navicular and cuboid.

METATARSALS.—The metatarsal proximal articulations are as follows:

I.—Chiefly with the entocuneiform, but by a small external facet with the second metatarsal.

II.—Only with the mesocuneiform proximally, but with the ecto- and entocuneiforms on the sides and, immediately distal to these, with the first and third metatarsals.

III.—With the ectocuneiform proximally, its proximoexternal angle reaching the cuboid but without a definite facet for that bone. Laterally with second and fourth metatarsals.

IV.—With the cuboid only proximally, third and fifth metatarsals laterally.

V.—(The bone itself unknown, but facets clearly displayed), with the cuboid by a small facet but chiefly by a large triangular facet on the fourth metatarsal which faces outward and downward.

This arrangement, strongly serial but not wholly primitive, is almost exactly that of *Dasypus* and other armadillos. It is variously modified in other, more specialized, edentates. In *Manis* the mesocuneiform is relatively larger, and the second metatarsal does not articulate externally with the ectocuneiform, while the fourth has a very strong ectocuneiform articulation, occupying about half of the distal surface of that bone.' In *Nothrotherium*, according to Stock, the fourth metatarsal has a strong ectocuneiform contact, while he shows *Mylodon* as having an opposite specialization in that the third metatarsal has a strong cuboid contact. *Hapalops* (Scott) seems not to have departed definitely from the primitive armadillos or palæanodont-like condition. In *Myrmecophaga* the fourth metatarsal has an ectocuneiform contact. In the tree-sloths the bones are fused.

With some specializations of their own, the metatarsals still show much resemblance to *Dasypus* in relative proportions. The first is reduced, less than half as long as the second. The second is the stoutest

of all, its distal end expanded and oblique. This is a generic specialization of *Metacheiromys*, as this bone is more normal in its proportions in *Palæanodon*. The third metatarsal, actually of about the same length as the fourth, is functionally longer by reason of the oblique tarsal articulations. Its proportions are about as in *Dasypus*. The fourth is similar in proportions to the third, but its proximal end is relatively narrower, its distal end more oblique.   Unlike *Dasypus*, it is both actually and functionally longer than the second. The fifth metatarsal is unknown, but its articulations are as in *Dasypus* and its proportions are probably similar.

The distal articular surfaces of the metatarsals are transversely cylindrical, with incomplete ventral keels, which are not, as in the metacarpals, flanked by pits. They are more primitive than in armadillos (most primitive of later edentates in this regard) in the slightly less developed keels and the slight transverse convexity of the surface as a whole.

Fig. 22. *Metacheiromys talusia* Osborn. First phalanx of second digit of left pes. Referred specimen, Yale Peabody Museum. A, Dorsal view. B, Internal view.   Natural size.

PHALANGES.—The first and second phalanges of IV and the second phalanx of III are relatively more elongate than in the fore feet, and these digits are in general more slender. The terminal phalanges are compressed claws like those of the fore feet, but much smaller and shorter, less strongly compressed. Some, at least, are lightly fissured.

The outstanding peculiarity of the pes is the specialization of the second digit, already alluded to in regard to the metatarsal. In the fragmentary Yale specimen of *M. dasypus*, listed above, there is a first phalanx of this digit. It is an extraordinary bone, short, stout, somewhat depressed, very oblique. The metatarsal articulation faces more upward than backward (although, by trial, this does not necessarily indicate a digitigrade foot as might be supposed) and consists of two unequal concavities with a sharp, deep posterior notch between them for the metatarsal keel. The distal articulation is deeply and rather squarely notched, the articular ridges on each side extending far onto the plantar part of the bone. Harmoniously, the proximal articulation of the second phalanx consists of two grooves, facing somewhat upward, with an irregular ridge between them. The distal articulation is a normal, broad, unkeeled groove.
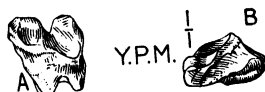
RELATIONSHIPS

The relationships of *Palæanodon* (and hence also of *Metacheiromys*) have been rather fully discussed by Matthew (1918). My own views differ from his in some respects, but are generally similar. Nevertheless, the evidence here presented (also known to Matthew but only in small part itemized by him) is so much more complete than that from *Palæanodon* alone, and general recognition of the latter has been so delayed, that a brief but comprehensive review may be of interest. It is presented with full recognition of Matthew's prior statement of many of the points involved, and of Osborn's still earlier recognition (1904) of the most essential feature. Further consideration of Wortman's views is unnecessary, the basis of his error having been fully explained above.

Palæanodon

As noted by Matthew, it is obvious that *Palæanodon* and *Metacheiromys* are closely related and that the differences between them are largely or wholly due to evolutionary advance. Careful comparison of all the known parts, some of the results of which have been stated above and others given by Matthew, reveals no feature in which *Metacheiromys* is more primitive than *Palæanodon* and none in which the difference is too great to have occurred, so far as may be judged by analogies in other groups, in a rather progressive line of descent in the available time: Gray Bull to Bridger B. The one possible objection, the three sacrals of Amer. Mus. No. 11549, is negatived by the knowledge of another sacrum of the same genus and a very closely allied species (Yale Peabody Museum No. 13502) which has our vertebræ and is in all respects like that of *Palæanodon* but slightly more advanced.

The chief advances, furnishing a valuable clue to the evolutionary direction followed by the group, are as follows:

1. The cheek teeth become further reduced and functionally replaced by the horny plates already present in *Palæanodon*.

2. The osseous bullæ, half-formed in *Palæanodon*, become complete; the external auditory meatus becomes ossified; the postglenoid region is further elongated, the mastoid further inflated.

3. The vertebral processes, at least in *M. dasypus*, become more produced.

4. The limbs become stouter, with stronger processes, the feet shorter, the digits more specialized in proportions.

5. The superior crest on the ischium becomes sharper, more prominent.

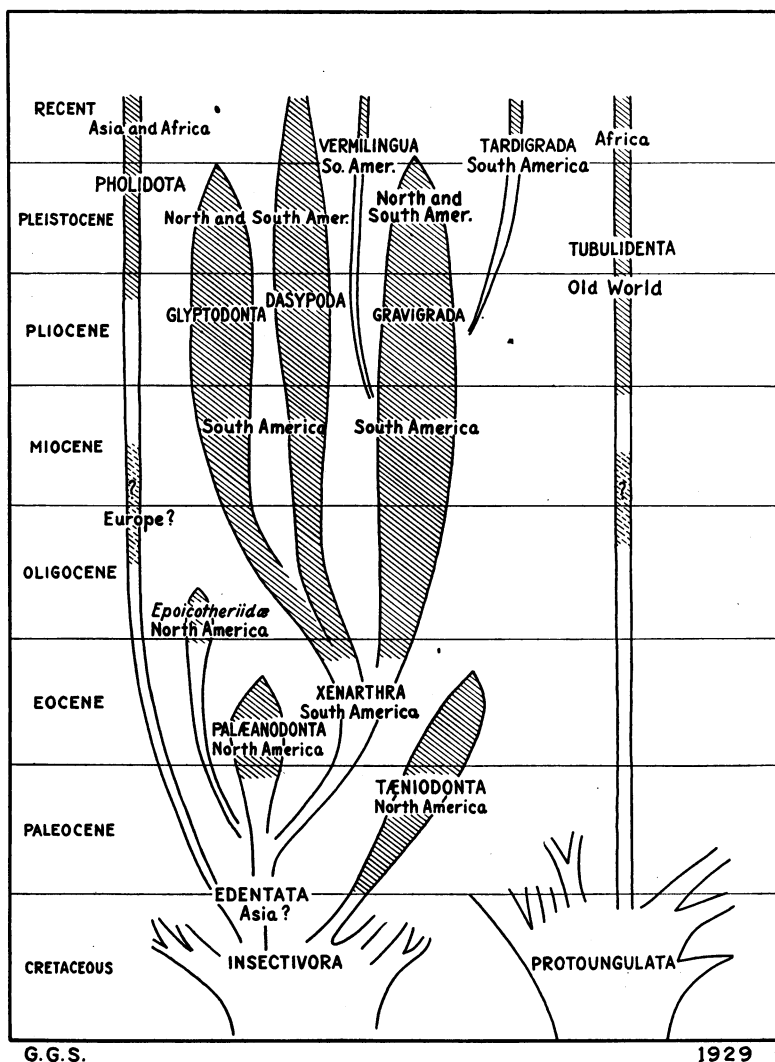6. The tarsus becomes slightly more armadillo-like.

Fig. 23. Phylogeny and distribution of edentates and supposed edentates.
Crosslined areas indicate known occurrences.

As Matthew has further emphasized, the probability that *Metacheiromys* is a descendant of *Palæanodon* is enhanced by the presence in the Wind River horizon of fragmentary remains intermediate in character between the two genera.

TÆNIODONTA

In the North American Paleocene and Eocene there occurs a sequence of at least four genera which are edentate-like: *Wortmania* (Puerco), *Psittacotherium* (Torrejon), *Calamodon* (Wasatch), *Stylinodon* (Bridger). Cope placed *Wortmania* ("*Hemiganus*") in the Creodonta, *Psittacotherium* in the Tillodontia, and *Calamodon* (+"*Ectoganus*") in the distinct group Tæniodonta. Marsh placed *Stylinodon* in the Tillodontia, and suggested the possibility of relationship between the Tillodontia and Edentata. Cope at first regarded the Tæniodonta as ancestral edentates, but he later seems to have considered this as possible but improbable.

Wortman (1896, 1897) recognized these four genera as closely related, united them in the family Stylinodontidæ Marsh, and placed them with the Conoryctidæ (*Onychodectes* and *Conoryctes*) in the new suborder Ganodonta, now considered as properly synonymous with Tæniodonta Cope. In a detailed discussion, he pointed out special resemblances to the ground-sloths, and he considered the direct derivation of these South American edentates from the Ganodonta as demonstrated.

If this were true, and the edentate relationships of the Palæanodonta granted, it would follow that the latter must be derived from early tæniodonts or at least very closely related to them. Some discussion of the tæniodonts is, therefore, necessary, although a detailed and complete review would be out of place here.

Wortman's view has been accepted by some workers, notably Schlosser (e.g., 1923, p. 496), but has been severely criticized and rejected by others, especially Scott (1904, p. 361; 1913, p. 625), Ameghino (1905, pp. 730–73, 5), and Winge (1915, pp. 300–301). Scott defers judgment as to the true affinities of the Tæniodonta but follows Osborn to the extent of tentatively considering them a distinct unguiculate order. Winge places them in the Insectivora as descendants of the Leptictidæ. Ameghino denied any affinity with the edentates and considered the tæniodonts as condylarths allied to the Periptychidæ.

In his discussion of *Palæanodon*, Matthew (1918, pp. 620–611) makes the following remarks:

"The Tæniodonta are also, in my opinion, probably an aberrant side branch of the primitive Edentata, and it may be possible in the future to unite the palæanodonts with this group. But at present I see no good evidence for such a step, and, pending re-examination of the tæniodonts, the present arrangement is less open to objection. The edentate affinities of the Metacheiromyidæ are much clearer than those of the tæniodonts, and they approach nearest to the armadillos, which are regarded by all authorities as the oldest and most primitive group of the undoubted Xenarthra. The tæniodonts were referred by Wortman to the edentates chiefly upon the evidence of resemblances between the stylinodonts and the ground sloths which I think must be explained in large part as convergent, since the sloth group appears to be a derivative of the armadillo group, and there are comparatively few points of affinity between stylinodonts and this more ancient group of the undoubted Xenarthra. The most earnest defender of Wortman's view must admit that there is a good deal of overstatement in his argument, and allow some justice in Winge's recent criticism. But it appears to the present writer that Wortman's critics have gone to the opposite extreme in their views."

In 1928 (pp. 957, 965) Matthew seems to have receded from even this limited acceptance of Wortman's thesis. He places *Onychodectes* and *Conoryctes* in the Insectivora as "transitional in some ways to the Tæniodonta." The latter he holds to be an "aberrant group paralleling ground-sloths," and says further, "whether the Tæniodonta can be considered a suborder of Edentata is open to question, but, if so, their relationship is more distant than that of the Pholidota. More probably they have none beyond a common descent from Cretaceous pre-Insectivora."

After re-examination of all the tæniodont originals of Marsh, Cope, and Wortman, and some new specimens, I believe that the following statements, essentially agreeing with Dr. Matthew's most recently published view, and in general agreement with Winge, are justified by present knowledge:

1. The tæniodonts are much less similar to the xenarthrans than are the palæanodonts.

2. Most of the resemblances to xenarthrans or palæanodonts are in habitus characters, indicative of convergence or parallelism.

3. The resemblances are largely outweighed by more deep-seated differences. It is a matter of opinion whether there is a residual resemblance, neither convergent nor merely primitive unguiculate or

insectivore in character, indicative of special affinity. If this is the case, however, the relationship must be very distant and due to an extremely remote common ancestry. The tæniodont line was distinct from that of the palæanodonts or xenarthrans at the end of the Cretaceous and was certainly ancestral to neither of the latter.

The essential points of the evidence are briefly presented:

1. Tæniodonts appear in the Puerco, already with their peculiar and non-palæanodont structure indicated, and their later history is contemporaneous with that of the palæanodonts, from which they diverge more and more.

2. Both in form and in number, the teeth have, and retain throughout their history, the clear stamp of an insectivore-like tuberculosectorial ancestry, already completely lost in the late Paleocene palæanodonts. The reduction in number is slight. The enamel is not reduced, and the teeth are progressive, not degenerate: the crowns remain completely enameled, and with the enormous elongation of the teeth the enamel extends far down in definite bands. The enamel is thick, its microstructure unique and not degenerate.[1]

3. I find no skull specializations which are in the least palæanodont-like, and only in superficial habitus characters is there a suggestion, even here remote, of some of the latest and most specialized edentates. Even in *Wortmania*, the earliest known tæniodont, the proportions and general structure of skull and jaws are clearly too specialized to give rise to those of palæanodonts or of primitive edentates. And, on the other hand, even the latest form, *Stylinodon*, is more primitive in some other features than the earliest known palæanodont or xenarthran. In all, the brain case is high and narrow, whereas it is relatively low and broad in palæanodonts and edentates. There is a lofty sagittal crest. The occiput is high and triangular. In *Stylinodon*, and hence presumably in all tæniodonts, the mastoid is not inflated, its ventral exposure is small, there are no osseous bullæ, the post-glenoid region remains as short as possible in a placental, the occiput beginning immediately behind the (unossified) external auditory meatus.

4. The cervical vertebræ (*Stylinodon*) are highly compressed, even more than in *Metacheiromys* or most later edentates, but beyond this habitus character, which is carried too far for an ancestral group, these vertebræ have no specifically palæanodont or edentate characters. The canals of the atlas are very different: there is a large, simple anterior

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[1] Thornton Carter, quoted by Matthew (1928), and confirmed by my own examination of new thin sections.

foramen for the nerve, and a very short, large, horizontal vertebrarterial canal or foramen, with a broad open groove running between the two. The vertebrarterial canal pierces all the cervicals, but is small on the seventh.

5.   The posterior dorsals (*Psittacotherium*) have metapophyses and anapophyses broadly similar to those of *Metacheiromys*, but these appear also in other groups, e.g., tillodonts, and may, therefore, be considered convergent if not accompanied by other and stronger evidences of affinity. The rib facets on the posterior dorsals are quite unlike those of *Metacheiromys*, being well separated and with the tubercular facets borne on high, strong pedicles.   The dorso-lumbar zygapophysial facets are strongly rounded and nearly vertical.

6.   In the fore limb are seen the most definitely edentate-like characters, and the main burden of Wortman's argument, so far as it is valid, depends on this part.   However, it is perhaps the most plastic and adaptive part of the whole skeleton in mammals and the most subject to complex convergence, so that if the resemblance is to be taken as indicative of affinity, it must either be very close and detailed or else accompanied by edentate-like characters throughout the skeleton.   Without minimizing the very striking character of the resemblance signalized by Wortman, it does not appear to me to be impelling as to affinities.   In part, as in the presence of a large entepicondylar foramen, or the presence of a stout clavicle, the characters are merely primitive.   In part, as in the deltoid crest or trochlea, the closest comparison is not with *Metacheiromys* or the primitive later edentates, but with the highly specialized Pleistocene ground-sloths.   These are characters related to fossorial adaptation and present in varying degree in all mammals of similar habits.   The carpus (so far as known in *Psittacotherium* and *Stylinodon*) rather strikingly resembles that of the ground-sloths, as emphasized by Wortman, but it is less like that of *Metacheiromys*.   There is a strong dorsal contact or unciform and lunar—a feature present in many mammals, but not in *Metacheiromys*.   Although Wortman does not show it so, the magnum was probably in contact with the second metacarpal dorsally, a condition primitive in most groups, but, as suggested above, probably not for edentates.

The metacarpals and phalanges (*Psittacotherium, Stylinodon*) are rather edentate-like so far as known, and are, therefore, also palæanodont-like.   The resemblances are chiefly that the metacarpals are stout, proximal and medial phalanges very short, the terminal phalanges great compressed claw-cores, the metacarpal articulations concave transversely,

keeled ventrally, the others simply pulley-like grooves. The specialization, even in *Psittacotherium*, is greater than in palæanodonts or most armadillos.

7.   The pelvis (*Psittacotherium*), considered by Wortman as strongly suggestive of edentate relationships, seems to me to offer strong evidence against his view. In the first place, it is obviously too highly specialized to be ancestral to any edentates except the most progressive sloths. And in the second place, it seems that its sloth-like characters are demonstrably convergent, even aside from phylogenetic difficulties introduced by the later existence of more primitive forms, for it has attained an ilium as expanded as in the most specialized recent genera without having any sign of the peculiarities of the ischium and of the pubic symphysis seen in the latter. In *Metacheiromys*, as one would expect in a true primitive relative of the Xenarthra, all of these characters are foreshadowed harmoniously.

8.   The hind limb is very imperfectly known. The femur is partly known in *Wortmania* and *Psittacotherium*, the tibia in *Wortmania*. The pes is almost unknown. The femur departs from the primitive insectivore type chiefly in its anteroposterior compression and in the third trochanter, which is much more proximal than in palæanodonts or most edentates.   The tibia is stout and strongly crested, but its distal end indicates a very shallow trochlear groove on the astragalus, and it has a prominent malleolus, not seen in *Metacheiromys*, and not, I believe, primitive for edentates.

In passing, it is noteworthy that the tæniodont structure as a whole is quite as much like that of the tillodonts as it is like that of any edentate, and there are some special resemblances both in skull and skeleton, although offset by equally significant differences.   The reason, I suppose, is somewhat similar to that for the tæniodont-gravigrade resemblance: similar habits of life and remote common ancestry in the Insectivora.

Epoicotherium

Epoicotherium ("*Xenotherium*" Douglass *non* Ameghino), from the lower Oligocene of Montana, was originally described as a monotreme (Douglass), and later referred to the Chrysochloridæ (Matthew, Gregory), but more detailed study indicates that it is an edentate (Zdansky, 1926; Simpson, 1927; Matthew, 1928).   It is the only edentate or edentate-like animal known from North America between the Middle Eocene and Lower Pliocene. Geographic and geologic considerations suggest that it

was derived from the Palæanodonta, but if so it must have been from a stage slightly more primitive than *Palæanodon ignavus*. This is the most acceptable hypothesis, but conclusive evidence either for or against it is lacking. The general skull form could be derived from the palæanodont condition, although it is shorter and broader, more wedge-shaped, the snout more depressed. Positive resemblances, aside from merely primitive characters, are seen in the degenerate one-rooted teeth, long, ridged and grooved palate, high narrow choanæ, ossified flask-shaped bullæ, relation of external auditory orifice to base of zygoma, very large inflated mastoids. It is more specialized than either palæanodont genus, or differently specialized, in numerous characters, including the union of pterygoid-alisphenoid crests with the bullæ, the development of a ledge above them, the transverse crowding together of the bullæ, the absence of a post-glenoid process, the confluence of the posterior lacerate and condylar foramina, and the difference in skull proportions already mentioned. The *Palæanodon-Metacheiromys* line does not foreshadow any of these characters. On the contrary, the earlier genera were trending away from the *Epoicotherium* type in several respects, most notably in the greater reduction of the teeth and their replacement by horny plates. Nevertheless, derivation of *Epoicotherium* from an unknown early palæanodont is a reasonable possibility, and seems more in accordance with the palæogeographic and phylogenetic evidence at hand than any other theory which can now be advanced.

XENARTHRA

Arguments against considering the Palæanodonta as related to the edentates (esp. Winge, Schlosser, quoted in introduction) do not deny that they are strikingly edentate-like, nor do they suggest any other line of relationship as closer, but insist that they are too highly specialized or too unequally specialized to be directly ancestral. This is certainly true, and everyone will grant Winge's argument perfect justice to this point. But to deny any relationship, or even rather close relationship, on this basis seems very illogical. Similar reasoning would, for instance, remove the titanotheres from the Perissodactyla, or, perhaps more nearly analogous, would deny any particular affinity between the inadaptive creodonts and the true carnivores. The palæanodonts are aberrantly specialized in several respects, and in others they may even have acquired particular edentate specializations earlier than they probably appeared in the ancestral xenarthrans. But Winge disregards the fact that they have, either typically developed or incipient, all the general

ordinal characters of the Xenarthra. Even in those characters which he cites as too primitive to accompany the high specialization in other parts, such as the lack of ischio-caudal symphysis or xenarthrous vertebræ, they show rather clearly the beginning of these specializations and are not merely primitive or generalized. Furthermore, some of the advances which he cites as prematurely specialized, such as the phalangeal articulations, are really definitely more primitive than in any later edentate. In still other points, such as supposing the toe proportions to be generalized, without suggestion of later edentate conditions, he is in error.

Throughout the osteological part of this paper, description has been facilitated by reference to various later edentates, particularly to the three most primitive groups, the armadillos, Miocene ground-sloths, and *Manis*. This has served to bring out much of the evidence. The more essential points of this evidence, both for and against edentate relationship for *Metacheiromys*, will be briefly recapitulated:

1. The dentition is edentate-like in its tendency toward reduction and the degeneracy of the cheek-teeth. It is more primitive than in any later edentate in retaining enamel on the canines. It is aberrantly specialized, with respect to the edentates, in the large cutting canines and presence of horny plates, and prematurely specialized in the reduction of the cheek teeth, which has gone further than in most later forms.

2. The proportions of the skull show none of the varied specializations seen in later edentates, save for the resemblance to *Dasypus* in the broad, low occipital region. This resemblance is probably convergent. The proportions show aberrant specialization in the elongation of the post-glenoid region, which is greater than in any other edentate.

3. The cranial foramina are largely insectivore-like, a type more or less nearly retained in *Manis*, Miocene gravigrades, and *Dasypus*, while some edentates show specializations apparently derived from a condition more like this. The closest resemblance which I have detected is with *Dasypus*, which has often been considered the most primitive recent xenarthran in this respect.

4. The character of the glenoid fossa and the retention of a small but typical post-glenoid process are more primitive than in any later edentates. The absence or small size of any other basicranial processes is edentate-like.

5. The large, compound, flask-shaped bullæ are paralleled in some later edentates, but prematurely[1] acquired in *Metacheiromys*. The presence of large entotympanics is very Xenarthra-like. The great

[1] That is, acquired too early for *Metacheiromys* to be ancestral to the later bullate forms.

expansion and inflation of the mastoids are aberrant specializations, correlated with the elongation of the post-glenoid region, tabular squamosal, broad occiput, etc., and broadly analogous to similar basi-cranial inflation in other orders, such as in the dipodids among rodents or some viverrines or mustelines among carnivores. These specializations are already indicated, but much less developed, in *Palæanodon*. They are functionally, but not structurally, paralleled in some later edentates, as *Myrmecophaga* and ground-sloths, in which the inflation is rather anterior than posterior to the auditory meati.

6. The brain of *Palæanodon*, so far as known, is much like that of *Manis*, still more like that of some armadillos, but apparently less advanced than in either.

7. The lower jaw is superficially Dasypoda- or Pholidota-like, perhaps convergently, in its long, slender horizontal ramus. In general structure it is more primitive and insectivore-like than in any later edentates.

8. The cervicals are primitive in being separate, with nerve exits, except the first, open; like most edentates in being short, low, and wide; specifically like the more primitive gravigrades (which I believe to be the least specialized Xenarthra in this region) in several features of the foramina, canals, and lateral processes.

9. The dorso-lumbar series is generally more specialized than in *Manis*, more primitive than in Xenarthra, but with some special re-semblances to the latter, even extending, in my opinion, to a foreshadow-ing of the xenarthrous articulations in the posterior dorsals and anterior lumbars.

10. The sacrum, similarly, is more specialized than in *Manis*, more primitive than in Xenarthra, but already advanced well beyond the generalized placental type in a definitely xenarthran way and harmoni-ously foreshadowing all the peculiarities of the xenarthran sacrum.

11. The tail is of primitive type, with a general resemblance to the more primitive armadillos.

12. The scapula has an eclectic series of xenarthran resemblances. General form, incipient second spine and coracoscapular notch, stout spine, and long acromion curving over the greater tuberosity are primi-tive xenarthran characters. The bifid acromion parallels some Xenarthra, but may have been independently acquired.

13. The humerus in general is very armadillo- or gravigrade-like. The distal articulation is rather more armadilloid, the deltoid crest and more general features of the distal end rather more as in early gravi-

grades. Except for the somewhat aberrant extreme development of the muscular crests, especially the supinator crest, it must nearly represent the common ancestral condition of these most primitive xenarthrans.

14. The radius and ulna are similarly suggestive of the generalized terrestrial xenarthran types, more primitive in a few respects, as the distal articulation of the ulna (more like *Manis*), aberrant or prematurely specialized in others, as the curvature of the ulna and extreme development of muscular insertions.

15. The carpus is more primitive than in *Manis* in the separate scaphoid and lunar, more primitive than in many Xenarthra in its more purely serial arrangement, unfused trapezium, and a few minor points. As cited in the description, there are some special resemblances to the Edentata as a whole, more to the most primitive Xenarthra.

16. Despite Winge, the proportions of the digits, both fore and hind, whether in a single foot or in comparison of fore and hind foot, are not generalized, but decidedly edentate-like, and more like the primitive Xenarthra than like *Manis*. The compressed claws of the fore-feet, more like the ground-sloths than the armadillos, are probably primitive for edentates. The metapodial and phalangeal articulations are strikingly armadilloid, but slightly more primitive. In a few particulars, such as the short, heavy second digit of the pes, *Metacheiramys* is aberrant, but *Palæanodon* is more primitive in this, and probably in all parts of the feet. The tendency towards ulnar rotation of the manus is distinctly Xenarthra-like.

17. The pelvis is unlike that of *Manis*, very like that of the Xenarthra, but more primitive. Xenarthran characters include the everted, strongly crested ilium, slender, relatively anterior pubis, short symphysis, large obturator foramen, deeper than long, everted ischia with dorsomedian crest. The fusion of one or two more caudals and the completion of the incipient caudo-ischial union would result in a typical but primitive and generalized xenarthran pelvic region.

18. The femur is very unlike that of *Manis*, suggestive of the armadillos but much less specialized, very close to that of the Miocene gravigrades but slightly more primitive in the less marked anteroposterior compression.

19. The crus differs from that of the armadillos only in being slightly more primitive. Thus, the tibia and fibula are unfused or only partly united. The anterosuperior tubercle is less expanded, the proximal part of the tibia is somewhat less produced anteroposteriorly, the distal end of the fibula less transverse, etc.

20. The astragalus of *Palæanodon* is approximately intermediate between a generalized insectivore type and that of the armadillos. In *Metacheiromys* the astragalus is still more definitely armadilloid, although primitive in not being quite as broad or oblique as in true armadillos. As shown in the descriptions above, the tarsus as a whole is decidedly armadilloid, but somewhat more primitive.

Considering the evidence as a whole, it seems to me to be conclusively in support of the view, first enunciated by Osborn, that *Metacheiromys* is definitely related to the Xenarthra and among these is most like the armadillos. Osborn was inclined to consider *Metacheiromys* as an armadillo, and he referred it to the Loricata. Since the armadillos are in several respects the most primitive Xenarthra, the matter is largely nominal, but I agree with Matthew in believing that the relationship is collateral to the Xenarthra as a whole and not specifically to the armadillos only. Reference to the Loricata seems excluded:

1. The loricate features of *Metacheiromys* are mostly those primitive for all Xenarthra. In those characters in which the early ground-sloths are more primitive than the armadillos, *Metacheiromys* is closer to the ground-sloths.

2. *Metacheiromys* is so early and primitive that the specifically xenarthran characters are indicated rather than typically defined, and the definitely loricate specializations are absent.

3. The *Palæanodon–Metacheiromys* phylum, although not widely divergent, is clearly progressing along a line of its own, away from the armadillos in some respects although paralleling them in others.

Recognition of Matthew's suborder Palæanodonta seems imperative. That the *Palæanodon–Metacheiromys* phylum, the only one known, was not *directly* ancestral to any Xenarthra is obvious and has been sufficiently emphasized. Nevertheless I believe that it more nearly retains and exemplifies the structure of that ancestry than do any other known mammals.

Such a conjecture has no absolute value, but, taking due cognizance of the characters which separate *Palæanodon* and *Metacheiromys* from each other and from a possibly ancestral xenarthran, I should judge divergence of the Metacheiromyidæ and of the pre-Xenarthra to have taken place in the Lower or Middle Paleocene. If the common ancestor were known, it would probably be most conveniently referable to the Palæanodonta.

PHOLIDOTA

Since Linnæan times, *Manis* has usually been closely associated with the South American edentates. A gradually increasing perception of its distinctive characters led to its separation from the xenarthran ant-eaters and to its being placed by itself in a taxonomic unit, "Squamata" or Pholidota, which was given successively greater value until it was made a distinct order by Weber. Several authorities, particularly Weber (1891, 1904, 1920), have emphasized the differences between *Manis* and the Xenarthra, differences very obvious even in the skeleton alone.

The view persists, however, that the Pholidota and Xenarthra are probably of remote common ancestry. If this is true, the Palæanodonta should be closer to that ancestry than other known mammals, and might be expected to give some definite evidence on the question. Matthew (1928) holds that they do. Without denying the probability that Pholidota and Xenarthra are distantly related groups, I feel, on the contrary, that the palæanodonts are definitely closer to the latter and as yet can throw little if any definite light on the origin of the Pholidota.

The same features, except those in the dentition, which exclude *Metacheiromys* from the direct ancestry of the Xenarthra also exclude it from the direct ancestry of the Pholidota. This does not apply with the same force to *Palæanodon*, which is sufficiently more primitive to have permitted Matthew (1918, pp. 653-654) to say, "So far as the skull is concerned, there is nothing to prevent our regarding *Palæanodon* as a direct ancestor of *Manis*." On the other hand, there is little evidence in favor of such a derivation. The reduction of the teeth and the long, ridged palate are *Manis*-like. The crania agree in so far as both are primitive or insectivore-like. I detect no manid specializations, and at least in *Metacheiromys* there is a resemblance rather to the Xenarthra than to *Manis*.

Most of the resemblances and differences throughout the skeleton have already been mentioned and will not be repeated. With few possible exceptions, the resemblances to *Manis* seem to be either (1) primitive placental or insectivore-like characters, or (2) specializations equally suggestive of the primitive Xenarthra and of *Manis*. In the first category would fall, for instance, the nominally nomarthrous vertebræ, in the second, the incipient ischio-caudal union (which is, however, more Xenarthra- than Pholidota-like) or limb and foot characters such as the peculiar proximal relationships of the fifth metacarpal. The existence of the latter sort of characters argues for the unity of the Edentata, a

unity which seems probable but not at all conclusively demonstrated, but not for close affinity between the Palæanodonta and Pholidota.

Many important characters have been pointed out in which *Metacheiromys* differs from *Manis* and resembles the Xenarthra. On this basis, the relationship to the latter would seem to be much closer than to the former. There seems little direct evidence for the view either that *Metacheiromys* is a derivative of the actual common ancestry of both Pholidota and Xenarthra, still less that, as suggested by Matthew (1918, p. 656), it was derived from the manid stock shortly after its separation from the xenarthran ancestry, unless some of the characters apparently primitive in the Pholidota are really secondary and derived from a much more clearly xenarthra-like condition. The anatomy of *Manis* is but little suggestive of such a history. The most definite evidence in its favor, but in my opinion also invalid or inadequate, is that based on the European Oligocene and Miocene bones which have been referred to the Edentata.

These European remains, described by Quenstedt (1885), Filhol (1893), Schlosser (1903, 1907), and Ameghino (1905, 1908), include the following:

Necromanis quercyi Filhol: Type, humerus from Bach. Femur from Mouillac referred by Ameghino. Considered a manid by both Filhol and Ameghino.

Leptomanis edwardsi Filhol: Type, part of top of skull from Larnagol. Placed in the Manidæ by Filhol. Referred by Ameghino to *Necrodasypus* and considered an armadillo, but compared also with *Orycteropus*, which is, he says, "un Tatou qui a perdu la carapace." Indeterminate, possibly an orycteropodid?

Palæorycteropus quercyi Filhol: Type, a humerus from Mouillac. Considered an orycteropodid by Filhol, a primitive armadillo by Ameghino, probably neither the one nor the other.

Necrodasypus galliæ Filhol: Type, dermal bones from Larnagol. Type of *Leptomanis* referred by Ameghino. Considered an armadillo by both Filhol and Ameghino. Scutes probably those of a lizard.[1]

Archæorycteropus gallicus Ameghino: Type, a tibia from Mouillac. Unnamed by Filhol, who compared it with *Manis* but held it to be indeterminate. Placed in the Orycteropodidæ by Ameghino, who also referred to the genus a fragment from the Patagonian *Notostylops* beds. Indeterminate.

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[1] A similar case of the very natural confusion of lizard dermal scutes with those of armadillos has occurred since this paper was originally completed. "*Loricotherium*" Weigelt, described as an edentate, was almost immediately shown by Weigelt himself to be a lizard. See Jahrb. d. Halleschen Verb. z. Erf. d. mitteldentschen Bodenschätze, etc., N. F. VIII, 1929, two papers.

Teutomanis franconica (Quenstedt): Types, humerus, radius, and ulna from a fissure at Solnhofen.   Named *Lutra franconica* by Quenstedt. Referred to *Potamotherium* by Schlosser in 1902.   In 1904, Schlosser referred to the species the distal end of another humerus, a broken femur, a calcaneum, and three metapodials, all also from Solnhofen.   He then considered the animal as an edentate, and compared it with *Manis* and with *Orycteropus*.   Ameghino restricted the trivial name to the types only, proposed a new generic name, and considered the beast a manid.

Teutomanis quenstedti Ameghino: Type, the fragmentary humerus referred by Schlosser to "*Lutra "franconica.*

Gallixtatus schlosseri Ameghino: Type, a metapodial from Mont Ceindre, near Lyons.   Ameghino referred to this species several median phalanges, rib fragments, an ischium, and a broken vertebra from the type locality, and he also referred the femur, calcaneum, and metapodials (called metatarsals by Ameghino, metacarpals by Schlosser) from Solnhofen which Schlosser had referred to "*Lutra*" *franconica.*

The specimens called *Leptomanis, Palxorycteropus, Necrodasypus,* and *Archxorycteropus* may safely be disregarded as indeterminate or definitely non-edentate.   The more important specimens have been refigured by Matthew (1918, after Schlosser and Ameghino) in such a way as to facilitate comparison with various edentates.[1]

Schlosser (1923, p. 496) says, "Immerhin zeigen diese dürftigen Reste, dass die Scheinbar so weit entferntstehenden Familien der *Orycteropodidx* und *Manidx* einerseits und der *Dasypodidx* anderseits höchst wahrscheinlich doch gemeinsamen Ursprungs sind." Matthew, although disregarding the orycteropodid resemblance, similarly suggests a rapprochement by these bones of the manids and the Xenarthra, through the palæanodonts.   "But this apparent simplification [in the limb bones of *Manis*] . . . may also be secondary, and that it is truly so seems to be quite definitely shown in the fossil Manidæ of the European Tertiary, in which intermediate stages are shown." (Matthew, 1918, p. 654).

After thorough study of all the literature and personal examination of the originals in Munich (through the kindness of Dr. Stromer), this conclusion seems to me to be unjustified.   It has not yet been shown that these bones did belong to manids.   They are unlike the same parts in *Manis* in many essential respects, and while intermediate stages are conceivable, there is no real evidence of their existence.   The confusingly eclectic but inexact resemblances of these fragments and isolated bones

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[1]In Matthew 1918, Fig. 64C, the lower figure is not the distal end of one of the metacarpals figured above it, but of a different specimen (type of *Gallixtatus schlosseri*) from Mont Ceindre, which is unlike Schlosser's specimen in several respects.

to *Manis, Orycteropus,* and dasypods are evidence of their inadequacy for real determination, rather than of their tending to link two or more of these groups. They are not intermediate in structure between *Palæanodon* and *Manis,* but about as specialized as the former and, except for habitus characters such as their stoutness and strong processes, specialized in a different way (in *Teutomanis* humerus, bicipital groove broad, rather than narrow, deltoid crest longer, not excavated in the same way, ectepicondyle shorter, supinator crest more curving, less plate-like; in ulna, olecranon equally long but bent quite differently; in metacarpals [*"Galliætatus"*], distal articulations keeled in quite a different manner; etc.).

It seems that the palæanodonts are not clearly related to *Manis,* that they do not tend to unite the Pholidota and Xenarthra, and that this theoretical union still lacks any definite palæontological support.

Origin of the Xenarthra

The order Xenarthra is characterized by the retention of many primitive characters, usually lost in at least the advanced members of other orders, together with certain specializations along peculiar lines, rarely or never seen in other placental mammals. Among the first may be mentioned the frequently large coracoid, the presence in some xenarthrans of a septomaxillary bone, relatively low type of brain, primitive genital organs, etc. Among the important specializations largely or wholly confined to this order are the xenarthrous vertebræ, the ischiocaudal union, the degeneracy of the teeth. Although highly varied, there can be no question that the group is a natural unit, and from its mingling of unusually primitive and peculiarly aberrant characters, it follows that it is a specialized and isolated offshoot from some very primitive stock.

So far all authorities seem to be in agreement, but as to the degree of separation from other mammals warranted by these facts and as to the character of the xenarthran ancestry there have been expressed the most varied opinions. Gervais (1858; *auct.* Weber, 1928, p. 170) proposed that they be considered as a separate subclass of mammals. Parker (1885, pp. 116–119) considered the edentates as nominally eutherian, i.e., placental, mammals, but as types more archaic than the Insectivora, well off the main line of mammalian ascent, and directly derived from the Prototheria. Thomas (1887, pp. 458–459) accepted Parker's conclusion quite literally, added his own theory that the most primitive mammals were homodont and monophyodont, concluded that this con-

dition is primary in *Dasypus*, and hence proposed to raise the edentates to a subclass Paratheria, of derivation quite distinct from that of placentals or of marsupials. He later withdrew this conception of dental evolution, however.

Ameghino (e.g., 1905, pp. 236–250), with reasoning not unlike that of Thomas, held that haplodonty, entelodonty (complete, closed tooth series), polyodonty, homodonty, and, in contrast with Thomas, diphyodonty or polyphyodonty are primitive for mammals and primary where found in cetaceans and edentates. He also stated that he found a perfect intergradation between the fossil edentates and the monotremes, and therefore united the Cetacea, Edentata, and Monotremata in a unit, Homalodonta, derived from the theromorph reptiles and contrasting with all other mammals. This view surely requires no refutation.

In his invaluable discussion of the maroscopic features of the brain in the edentates, G. Elliot Smith (1899) directed specific attention to the status of the supposed Subclass Paratheria, concluding that the evidence of the brain decisively controverted this arrangement and that the Xenarthra were derived from primitive placentals. Largely on the evidence of *Myrmecophaga*, he suggested affinities with the primitive Carnivora.

It seems possible to reconcile this view with that here advocated, for, like most of its other anatomical features, the brain of *Myrmecophaga* is somewhat more advanced than that of the armadillos, and I question whether its peculiarities are more specifically creodont-like, except convergently, than proto-insectivore-like. Furthermore, the primary fact of common placental origin, so much stressed, is indisputably in accord with the palæontological evidence then lacking but now supplied. Elliot Smith concluded that "the Armadillos separated themselves from the others at a very early period, and underwent extreme bodily modifications of a protective nature in order that they might be able to escape extinction, because their brains had become reduced to the lowly standard of the Insectivora." *Metacheiromys* suggests that the last phrase might better read "had remained at the lowly standard of the Insectivora."

Scott (1903, p. 3) proposed to accept Thomas' view in placing the edentates in a distinct subclass, but he did not accept the only specific basis for that view, the theory of dentition which had meanwhile been withdrawn, nor did he give any additional reasons for such an extreme stand, nor controvert the opposing arguments of Elliot Smith and others. He did draw very valuable conculsions as to the mutual affinities of the

various edentates, but considered the group as a whole of unknown origin.

Chiefly because *Orycteropus* lacks various xenarthran specializations, a fact now conceded to be due to lack of affinity, Winge (1923) regarded the Xenarthra as directly derived from the Orycteropodidæ— the converse of Ameghino's disposition of *Orycteropus* as an armorless armadillo.

Orycteropus has not been especially considered in the present paper because *Metacheiromys* shows no particular tubuli-edentate characters. The evidence admirably summed up in the recent monograph by Sonntag and others (1925–26) seems to prove that *Orycteropus* has no special affinity with *Manis* or the Xenarthra. The characters of *Metacheiromys* are in agreement with this view.

Matthew, finally, regards the edentates as derived from unknown, probably Holarctic, insectivores allied to the Leptictidæ and Pantolestidæ (1918, pp. 656–657).

Into this confusion *Metacheiromys* seems to bring order. Aside from the dentition, it offers a striking and adequate transitional stage from the primitive placental or insectivore skeleton to that of the Xenarthra in almost all characters. In such crucial points as the cranial foramina or the structure of the astragalus, it seems to point clearly to the Insectivora.

Such xenarthran characters as the presence of a septomaxillary or the rather archaic genital organs are readily explicable as inherited from late Cretaceous placentals which were inevitably much less specialized than the living Insectivora with which Parker, for example, made comparisons. The complete description of *Metacheiromys* here offered gives, in my opinion, conclusive support to Matthew's view that the Xenarthra were derived from the Insectivora, for *Metacheiromys* seems clearly related to the former, and yet is also very suggestive of immediate derivation from the latter.

The opposite view, that of subclass distinction for the edentates, has found, and I believe can only find, its chief support in the dentition. Here *Metacheiromys* is of little help, but the abandoned views of Thomas (and those of Ameghino) depended on theoretical considerations which would not now be urged by anyone familiar with the palæontological evidence. It is now beyond reasonable doubt that the most primitive mammals were heterodont and diphyodont, that homodonty and monophyodonty are always secondary where they occur among mammals. The conditions tending to link the Xenarthra with the other mammals cannot be progressive, but vestigial. This includes the diphyodonty of *Tatu*, vestigial enamel organ in armadillos, occasional presence of pre-

maxillary teeth, vague heterodonty in some sloths. Nor can divergent characters, such as the polyodonty of *Priodontes*, for instance, be primitive. There is ample analogy for such reduplication of teeth (especially when degenerate) by secondary proliferation from the dental lamina in an abnormally elongate jaw. These are indications of the fact, to which general consideration of their anatomy would force one in any event, that the Xenarthra once possessed teeth of normal eutherian number, structure, and succession. Their degeneration, a habitus character conditioned by diet, was one of the first specializations of the order.

RÉSUMÉ OF EDENTATE RELATIONSHIPS

The evidence given in the present paper and in the works cited leads to the following views as to edentate relationships:

1. The family Metacheiromyidæ is closely related to the Xenarthra. Although this phylum is aberrant in some respects, its divergence from that ancestry is relatively slight, and it nearly represents the primitive xenarthran structure.

2. *Epoicotherium* is of uncertain origin, but the most plausible hypothesis is that it represents an independent offshoot from Paleocene Palæanodonta.

3. The tæniodonts do not represent the ancestry of all or part of the Xenarthra, but are probably a partly convergent line of very remote common ancestry.

4. The manids are possibly of common origin with the Xenarthra, but if so their division from that group was more ancient than that between the metacheiromyid ancestry and the xenarthran ancestry.

5. The supposed edentates of the Oligocene and Miocene of France and Germany are of uncertain position. They do not support the view of Filhol and Ameghino that xenarthrans were then present in Palæarctica. They are not surely manids, and are inadequate bases for the supposed rapprochement of manids and Xenarthra or Palæanodonta (Matthew, Schlosser), although this may eventually prove to be correct.

6. Although it does have many striking resemblances to the Xenarthra and Pholidota, it now seems probable that *Orycteropus* is not related to these groups but is a very ancient derivative from the protoungulate stock.

7. The xenarthrans are a unified group of common origin, probably derived in the late Cretaceous or early Paleocene from the Palæanodonta, which in turn were derived from Cretaceous Insectivora.

8. Primary division of the Xenarthra was into two branches, Loricata and Pilosa of Flower, Hicanodonta and Anicanodonta of Ameghino. The armadillos are the most primitive of Loricata, the gravigrades the most primitive of Pilosa. In some, but not all, respects the armidillos are more primitive xenarthrans than the gravigrades.

These views are incorporated in the accompanying diagram (Fig. 23).

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