To Susan Koelle
With my regards
R J Emry

A NORTH AMERICAN OLIGOCENE PANGOLIN AND OTHER ADDITIONS TO THE PHOLIDOTA

ROBERT J. EMRY

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 142 : ARTICLE 6 NEW YORK : 1970

A NORTH AMERICAN OLIGOCENE PANGOLIN AND OTHER ADDITIONS TO THE PHOLIDOTA

ROBERT J. EMRY
Department of Geology
Columbia University
New York

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 142 : ARTICLE 6 NEW YORK : 1970

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 142, article 6, pages 455—510, figures 1–32

Issued November 5, 1970
Price: $2.50 a copy

This article completes Volume 142

Printed in Great Britain by Lund Humphries

CONTENTS

INTRODUCTION 459
Acknowledgments 459
Abbreviations 459
LIVING AND FOSSIL PANGOLINS 460
Living Pangolins 460
Pleistocene Fossil Pangolins 461
European Tertiary Pangolins 461
A North American Tertiary Pangolin 465
ORDER PHOLIDOTA WEBER, 1904 465
Family Manidae Gray, 1821 465
Patriomanis, New Genus 465
Type: *Patriomanis americanus*, new species 465
Diagnosis 465
Distribution 466
Patriomanis americanus, new species 466
Type: F:A.M. No. 78999 466
Locality and Stratigraphic Position 466
Description 466
Skull 466
Brain 471
Vertebrae 471
Cervicals 472
Dorsals 472
Lumbars 472
Sacrum 472
Caudals 472
Pectoral Girdle 473
Forelimb 473
Humerus 475
Ulna 478
Radius 478
Manus 480
Pelvic Girdle 481
Hind Limb 481
Femur 481
Tibia 481
Fibula 482
Pes 482
Measurements 483
Summary 484
PANGOLIN ANCESTORS 486
Palaeanodont Characters and Comparisons 487
RELATIONSHIPS 502
Palaeanodont-Xenarthran Affinities 502
Xenarthran Affinities 503
Palaeanodont-Manid Affinities 503
PHYLOGENY AND TAXONOMY 506
Metacheiromyidae Wortman, 1903 506
Epoicotheriidae Simpson, 1927 506
Manidae Gray, 1821 506
CLASSIFICATION OF THE ORDER PHOLIDOTA 507
REFERENCES 507

INTRODUCTION

THE STUDY THAT LED to the present report began when a cranium and associated postcranial elements from Chadronian deposits near Alcova, Wyoming, were recognized as those of a pangolin—the first, and so far the only, evidence that representatives of the Manidae once lived in the New World.

The fossil was collected in 1957 by a Frick Laboratory field party under the leadership of Morris F. Skinner, but was not recognized in the field as a pangolin. Because the cranium lacked distinct crests and the sutures between bones were distinct, its field label read "immature ? carnivore." When I began a study of the collection from the Alcova area, the specimen again came to light. The general form of the cranium suggested that of an anteater, but it was still not recognized as a pangolin until unfavorable comparisons with recent myrmecophagids led, more by accident than by design, to an adjacent tray containing a skeleton of *Manis pentadactyla*. The fossil cranium was similar to that of the living pangolin, but disbelief prevented a definite judgment until all the available postcranial elements associated with the fossil cranium were also found to exhibit characteristic pangolin features.

Subsequent to this discovery, the study was somewhat anticlimactic but interesting and far-reaching nevertheless. A survey was made of the literature on the previously known fossil manids. These fossils, as well as the living species of *Manis*, are briefly discussed in the present report. A reappraisal of the metacheiromyids led to changes in taxonomy at the suborder level when they were shown to be ancestral to the Manidae, which has long been an orphan family in mammalian classification.

ACKNOWLEDGMENTS

My first expression of appreciation should be to the late Mr. Childs Frick, without whose support and guidance in field work the fossil herein described would probably never have been collected. I am also grateful to Morris F. Skinner for making certain, as he always does, that the specimen had detailed stratigraphic and geographic data, without which its value would be greatly diminished.

I thank the staff of the Department of Vertebrate Paleontology of the American Museum of Natural History for the use of the fossil collections and other facilities, including a place in which to study. Dr. Malcolm C. McKenna, as my sponsor, has provided direction through many comments and suggestions, and special thanks are due both to him and to Dr. Richard Tedford for improvements in the present paper as a result of their critical reading of the manuscript.

The Department of Mammalogy of the American Museum of Natural History has permitted me to study recent mammals in their collections. I particularly appreciate the opportunity to study the large number of specimens of all of the species of living pangolins.

For the opportunity to study fossils from other institutions I thank the following persons: Dr. Donald E. Savage of the University of California at Berkeley for lending me fossil myrmecophagans, and Dr. Albert E. Wood of Amherst College for lending me *Palaeanodon* material and for permission to illustrate the humerus of *Palaeanodon woodi*.

All of the photographs of figures 8–10 and 15 were made by Mr. Chester Tarka, who also gave me valuable advice for making the remainder of the stereophotographs for which I take criticism or credit. All of the line drawings not credited to other sources were made by Mr. Raymond Gooris. The restoration drawing of the humerus of the new fossil pangolin (fig. 15C) was made by Miss Biruta Akerbergs.

My wife, Susan, deserves special thanks for typing the several revisions of the manuscript.

The research for this report was carried out during my tenure as a Fellow of the Faculty of Pure Science of Columbia University with a National Science Foundation Graduate Fellowship.

ABBREVIATIONS

The following abbreviations are used to designate institutional collections.

A.C., Amherst College
A.M.N.H., the American Museum of Natural History, Vertebrate Paleontology
A.M.N.H. (M.), the American Museum of Natural History, Mammalogy Collection
F:A.M., Frick American Mammals, the American Museum of Natural History

LIVING AND FOSSIL PANGOLINS

A FRAMEWORK and perspective for the description of the new form can best be given by a brief discussion of the living species of pangolins and a historical review of the previously known fossils of the family Manidae.

LIVING PANGOLINS

There is general agreement among most workers that there are seven distinct and well-defined species of living pangolins, but the number of genera to which these have been assigned has varied widely. Pocock (1924) seems to have been the most extreme splitter, assigning the seven species to six genera and three subfamilies. Simpson (1945, p. 195) considered Pocock's arrangement to be "only an extreme instance of unnecessary and inconvenient taxonomic inflation, giving generic rank to each of the good species of one genus," as "all seven species are actually very much alike."

The living pangolins are not so uniform in morphology as is supposed by some workers who have evidently made comparisons with only one species, usually *Manis javanica*, and assumed that it was representative of all the living species. In the literature there are many statements about *Manis* (e.g., "*Manis* has no lacrymal bone") that are violated by one or more of the living species.

Three of the living species are confined to Asia: *Manis pentadactyla*, now living in India and Ceylon; *M. javanica*, in southeast Asia to Borneo and Java; and *M. aurita*,[1] ranging from Burma through southern China to Formosa and Hainan. The other four species are restricted to Africa. Three of these, *M. gigantea*, *M. tricuspis*, and *M. tetradactyla* (=*M. longicaudata*), coexist in western and central Africa. The other, *M. temminckii*, ranges through the southern and eastern parts of the continent.

Pocock's (1924) classification was based primarily on differences in external characters. These differences are included with others from various sources and personal observations and can be listed as follows: The three Asiatic species have small external ears (pinnae); these are totally lacking in the four African species. The xiphisternum of the three Asiatic species is a short, expanded, spade-shaped plate; the four African species show an elongation of the xiphisternum into two branches extending backward to the level of the last ribs. The Asiatic species have a median symmetrical row of scales that continues to the end of the tail; but in the African species this row splits on the tail into two rows of asymmetrical alternating scales. The fifth digit of the rear foot of the Asiatic species is as large as the first; in the African species it is very much reduced. The Asiatic species have bristles between the scales of the tail; these are lacking in the African forms. This is surely not an exhaustive list of the differences between Asiatic and African groups of species, but should be sufficient to indicate that the pangolins of different continents are quite distinct in a number of characters.

In addition to the differences between the species from different continents there are other differences among species from one continent. The three Asiatic species seem to be more uniform than the four from Africa. *Manis tricuspis* and *M. tetradactyla* (=*M. longicaudata*) differ from all other species in several features: The eyes are distinctly larger; the lacrimal bone is present; hair is present on the upper sides of the feet; the tail is much longer; the first digit of not only the forefeet but also the hind feet is very much reduced in size; and the epitympanic recess is decidedly more inflated laterally and posteriorly in the squamosal bone (compare figs 8B and 9B with fig. 26). Some of these features may be related to the arboreal habits of these two species. Of the four African species only these two have an unscaled terminal pad at the end of the tail. This feature, however, is also seen in one Asiatic species, *M. javanica*, which moreover has the longest tail among the three Asiatic species.

Manis temminckii differs from all other species in the complete loss of the entepicondylar foramen of the humerus. The entepicondyle shows no sign of the bar of bone which in all other species forms the anterior side of this foramen. This condition was noticed in one specimen and thought to be an individual anom-

[1] Pocock (1924) stated that the three pangolins of Asia are *Manis crassicaudata*, *M. javanica*, and *M. pentadactyla*, and that *M. aurita* is a synonym of *M. pentadactyla*. Frechkop (1931) and other workers since that time have listed the three Asiatic species as I have.

aly, but such is not the case. The foramen is lacking in all the specimens of *M. temminckii* in the mammal collection of the American Museum of Natural History.

A thorough study of all the living pangolins would no doubt add many more differences to those noted above, and the significance of these differences in terms of relationships and taxonomy cannot be adequately interpreted until such a study has been completed. Pocock (1924) probably attached too much taxonomic significance to the characters he observed, but it seems equally extreme to reduce his six genera to one. In my opinion the number of genera should be somewhere between these extremes. The three Asiatic species seem to be different enough from those of Africa to warrant generic distinction of these two groups and the four African species could possibly be further subdivided at the subgeneric (if not the generic) level.

Because the number of genera to which the living species are assigned in no way affects my conclusions, I will consider, for purposes of the present paper, that the living species all belong to one genus, *Manis*. My previous comments show that my convictions are otherwise, but the assigning of the species to other genera is deferred because this should follow a more thorough study than is practical here.

PLEISTOCENE FOSSIL PANGOLINS

Extinct species of the genus *Manis* are known from the Pleistocene of Asia, but these differ so little from the living species that they shed little light on the history of the group. *Manis lydekkeri* Dubois, 1908, from the Carnul Caves of India, is based on an isolated phalanx. *Manis palaeojavanica* Dubois, 1907, which is larger than any of the living species, is the best-known fossil pangolin (see Dubois, 1907, 1908, 1926; Hooijer, 1947, 1961; Harrisson, Hooijer, and Medway, 1961; and other references within these). This fossil form has been found in association with one of the present-day species, *Manis javanica* (Harrisson, Hooijer, and Medway, 1961).

EUROPEAN TERTIARY PANGOLINS

The first fossils from the European Tertiary to be recognized as manids were those described by Filhol (1894) from the Phosphorites of Quercy.

Necromanis quercyi Filhol is based on a humerus from Bach (fig. 1). Filhol observed the characteristic distal elongation of the deltoid crest[1] and the manner in which this crest was folded over toward the medial side of the bone. This feature, along with a general correspondence of this bone in other respects to the humerus of *Manis*, left little doubt as to its affinities. The only discrepancy noted by Filhol was that the profile of the trochlea in the fossil was convex, rather than concave as in *Manis*. Had he compared the fossil bone with other than one species of recent pangolin, even this difference would not have appeared abnormal because, as Guth (1958) pointed out, in *M. tetradactyla* (=*M. longicaudata*) the profile of the trochlea is convex, but in *M. pentadactyla* and *M. javanica* it is concave.

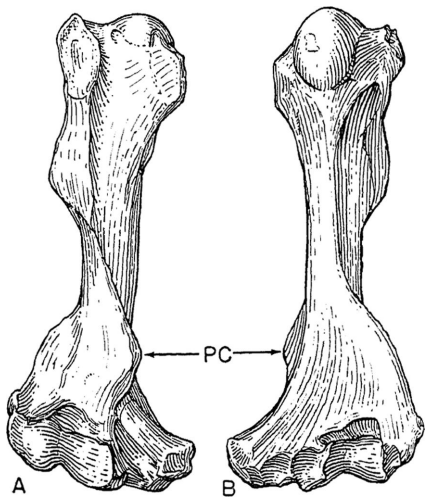

FIG. 1. *Necromanis quercyi*, type, right humerus from Phosphorites at Bach, France. A. Anterior view. B. Posterior view. PC, pectoral crest. ×1. (After Filhol, 1894, figs. 1 and 2.)

Leptomanis edwardsi Filhol was based on the top part of a cranium with nasal bones from Larnagol. The general configuration of the skull and relationships of the nasal bones to the frontals led Filhol to conclude that the animal was a manid. The specimen is so imperfect that this allocation has been subject to some doubt. Simpson (1931) considered it "indeterminate, possibly an orycteropodid?" But manid remains are known from similar deposits of similar age in the same area, and as the few features observable

[1]The distally elongated part of this process is actually the pectoral crest, as in *Manis*, but Filhol and other authors since that time have referred to it as the deltoid crest.

on this specimen compare more favorably with *Manis* than with any other known mammal, its inclusion in the Manidae is justified. That it is generically distinct from *Necromanis*, or, indeed, if it is even a manid, can be determined only by the discovery of more complete and associated material. Until then it will have to be retained in the Manidae with the understanding that its real identity may not be known.

Almost a decade before Filhol described the two genera from the Phosphorites, fossil manid bones had been found and described by Quenstedt (1885), but he did not recognize that these were of a manid. He gave the name *Lutra franconica* to a humerus, radius, and ulna from a Miocene (probably Burdigalian) fissure filling at Solnhofen (figs. 2, 28D). In 1904, Schlosser referred to this species the distal end of a humerus, a broken femur, a calcaneum, and three metapodials, also found at Solnhofen (figs. 3, 30E, 32C). At that time he believed these to be the bones of an edentate and referred them to that order, but did not change the generic name. Ameghino (1905) studied these remains along with additional non-associated material from the Miocene of Mont-Ceindre near Lyons, France. He restricted the trivial term, *franconica*, to the type described by Quenstedt and proposed for it a new generic name, *Teutomanis*. The humerus that was referred to "*Lutra*" *franconica* (now *Teutomanis franconica*) by Schlosser was made the type of a new species, *Teutomanis quenstedti*, by Ameghino.

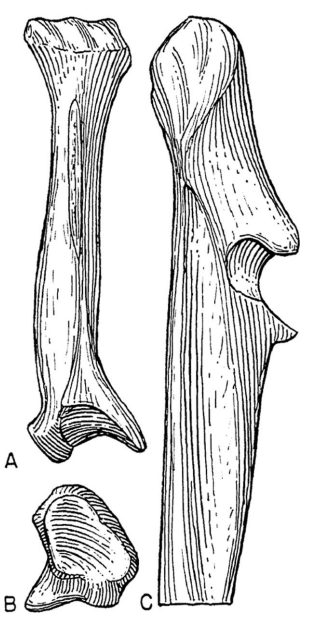

FIG. 2. *Teutomanis franconica*, radius and ulna of type, from Miocene (probably Burdigalian) fissure filling at Solnhofen, Germany. A. Left radius, lateral view. B. Left radius, distal view. C. Left ulna, medial view. Type also includes left humerus (fig. 28D). All ×1. (After Quenstedt, 1885, pl. 2, figs. 18–20.)

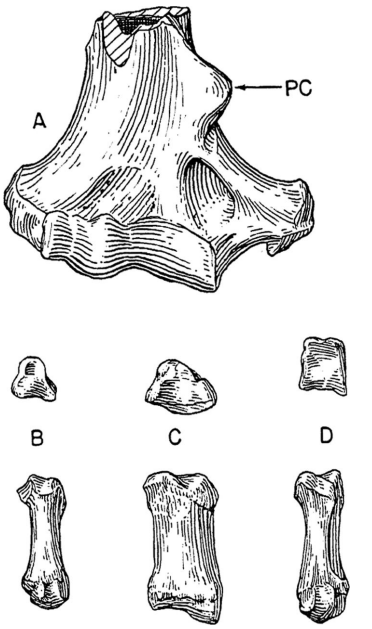

FIG. 3. *Teutomanis quenstedti*, from Burdigalian fissure filling at Solnhofen, Germany. A. Type, distal part of right humerus. PC, pectoral crest. B, C, D. Metacarpals, proximal and posterior views. See also part of right femur (fig. 30E) and calcaneum (fig. 31C). All ×1. (After Schlosser, 1904, pl. 26, figs. 4, 8–10, 14.)

The femur, calcaneum, and metapodials which Schlosser had also referred to "*Lutra*" *franconica* were referred by Ameghino to a new genus and species, *Galliaetatus schlosseri*, which he had erected on the basis of a metapodial from Mont-Ceindre, and which he considered to be an armadillo.

Schlosser (1907) argued that the humerus (made the type specimen of *Teutomanis quenstedti* by Ameghino), and the femur, calcaneum, and metapodials (referred by Ameghino to *Galliaetatus*) were derived from one individual and that the foot bones were metacarpals and not, as Ameghino had said, metatarsals. But Ameghino (1908) strongly contested this opinion and stated that it would be (freely translated)

"quite paradoxical for an animal with the humerus of a manid to possess a femur, calcaneum, and metacarpals having all the characters of a dasypodid." The dispute was apparently never resolved. Schlosser and Ameghino, however, were in accord on one point—that the metapodials from Mont-Ceindre and those from Solnhofen were from the same kind of animal.

In the light of accumulated evidence, *Teutomanis* and *Galliaetatus* can confidently be considered synonymous. The evidence can be summarized as follows: (a) Schlosser's statement that the bones were all of the same individual; (b) the statement by Viret (1951, p. 102) that not only in the region of Solnhofen, but also in the regions of Lyons and Eichstatt, the digits of

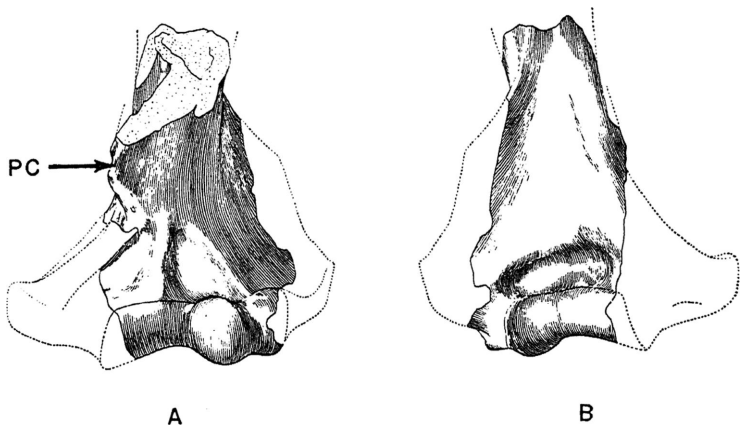

FIG. 4. Cf. *Teutomanis*, distal end of left humerus from middle Stampian of St. André, near Marseilles, France. A. Anterior view. B. Posterior view. PC, pectoral crest. × 1. (From Helbing, 1938, fig. 1.)

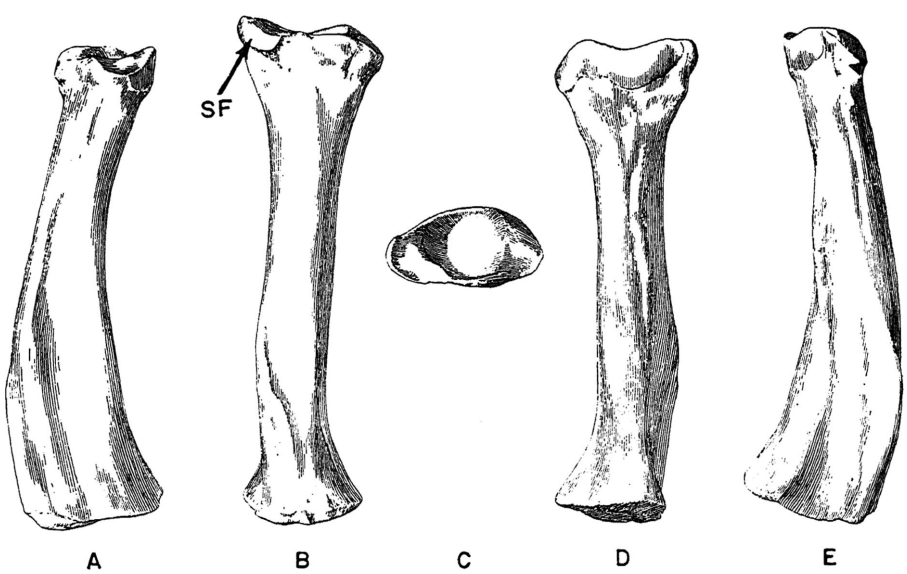

FIG. 5. Right radius of manid (probably *Teutomanis*) from upper Aquitanian of Montaigu-le-Blin (Allier), France. A. Medial view. B. Anterior view. SF, "sesamoid" facet. C. Proximal view. D. Posterior view. E. Lateral view. × 1. (From Helbing, 1938, fig. 2.) In Helbing's figure this was identified as a left radius and the medial view was labeled lateral view ("von aussen") and the lateral view labeled medial view ("von innen").

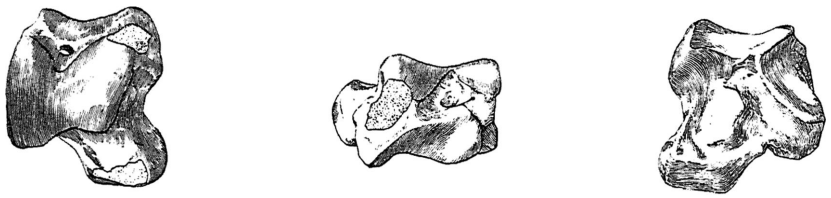

FIG. 6. Right astragalus of manid (probably *Teutomanis*) from upper Aquitanian (Hydrobienkalk) of Weisenau near Wiesbaden, Germany. A. Anterior view. B. Proximal view. C. Posterior view. × 1. (From Helbing, 1938, fig. 3.)

"*Galliaetatus*" are associated with the humerus of *Teutomanis* and not with the humerus of a dasypodid; (c) the lack of any other definitely xenarthran bones anywhere in the Old World; (d) evidence put forth by Guth (1958) and discussed later in the present report; and (e) evidence from the new Oligocene pangolin described later in the present report. *Teutomanis* and *Galliaetatus* are herewith considered synonymous, with the surviving generic name being *Teutomanis*.

After Ameghino and Schlosser, the next report of a Tertiary fossil manid was by Dehm (1937), who described the distal portion of a humerus and part of an ulna from a Burdigalian fissure filling at Wintershof-West, near Solnhofen. These fossils were not figured, but according to his description the humerus has the distinctive development and distal elongation of the deltopectoral crest seen in *Manis*. He concluded that the bones are morphologically similar to, but decidedly smaller than, *Teutomanis franconica*.

Helbing, in 1938, reviewed the previous records of European Tertiary pangolins and also described additional remains. The distal end of a humerus (fig. 4) from the middle Stampian of St. André, near Marseilles, regardless of the damage, shows diagnostic features that justify its allocation to the Manidae. Its morphology is most like that of *Teutomanis franconica*.

A radius (fig. 5) from the upper Aquitanian of Montaigu-le-Blin (Allier), according to Helbing (1938, p. 299), shows important differences from that of *Manis*; the proximal end is wider and the distal part of the shaft is less laterally compressed. He interpreted this as being a "primitive state," an interpretation confirmed by Guth (1958), who stated that an unpublished study of a more complete skeleton from the upper Aquitanian of the Allier Basin showed that the radius really belongs to a pangolin.

The other bones described by Helbing were an astragalus and calcaneum (figs. 6 and 7) from the upper Aquitanian (Hydrobienkalk) of Weisenau near Wiesbaden. These two bones also differ in important features from the same bones of *Manis*. The calcaneum is similar in size and morphology to that of *Teutomanis franconica*

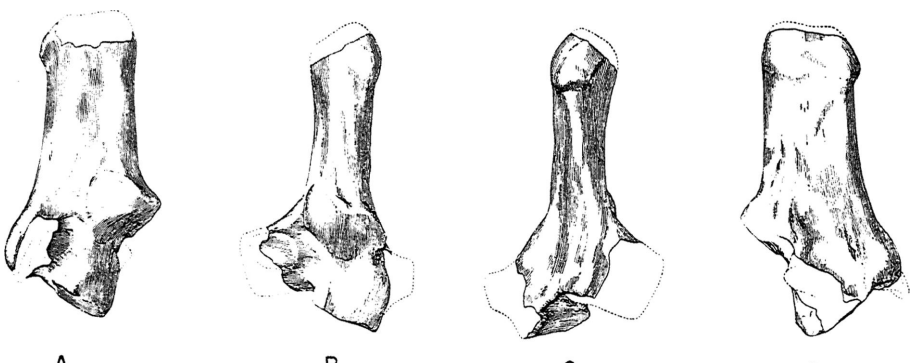

FIG. 7. Cf. *Teutomanis*, left calcaneum, from same locality as astragalus, figure 6. A. Medial view. B. Anterior view. C. Posterior view. D. Lateral view. × 1. (From Helbing, 1938, fig. 4.)

(*Galliaetatus* of Ameghino). The trochlea of the astragalus is more asymmetrical than that of *Manis*. But here again, Guth (1958) confirmed that these bones are of a pangolin by referring to the unpublished study mentioned above.

The next report of a fossil manid was by Viret (1951), who described a humerus from the Miocene (upper Vindobonian) of La Grive Saint-Alban. This bone is of a young individual with the proximal epiphysis unfused and missing and the distal extremity broken away. Enough remains to show the characteristic elongation of the delto-pectoral crest as far distally as the upper end of the entepicondylar bridge and the tendency of this crest to turn over medially. On this basis the bone can be allocated unequivocally to the Manidae. Viret commented that the humerus resembles that of *Necromanis quercyi*, but when adult would probably compare more favorably in size with that of *Teutomanis franconica*.

In Europe, the youngest fossil referred to the Manidae is a bifid distal phalanx described by Kormos (1934) from the Villafranchian of Villany in Hungary. Guth (1958), in his discussion of fossil manids, remarked that this phalanx is so characteristic that there can be little doubt it was that of a manid. Other than its late occurrence, it sheds little light on the post-Miocene history of pangolins in Europe.

The fossil record of pangolins, although meager, is sufficient to establish beyond doubt that these animals were living in Europe during the Oligocene and Miocene. These forms differed from recent pangolins in several features that are important links to their ancestry. In general, the limb bones are more angular because of the more sharply defined muscular crests. Helbing (1938) pointed out differences in the radius, calcaneum, and astragalus. The metapodials have the distal keel developed only ventrally rather than continuing over the distal end and onto the dorsal face as it is in *Manis*. The femur has a third trochanter and a digital fossa, characters lacking in *Manis*.

A list of the names applied to the manid remains of Europe is as follows:[1]

Necromanis quercyi Filhol, 1894
Leptomanis edwardsi Filhol, 1894
Teutomanis franconica Quenstedt, 1885
Teutomanis quenstedti Ameghino, 1905 (=*Galliaetatus schlosseri* Ameghino, 1905)
Manis hungrarica Kormos, 1934

Approximate known time ranges of these genera are given in the final section of the present report. The only one of these genera known from more than one specimen is *Teutomanis*. Most of the specimens are not diagnostic enough to be assigned to species, so the time ranges of species cannot be given.

A NORTH AMERICAN TERTIARY PANGOLIN

The single specimen of a North American Oligocene pangolin exhibits most of the characters seen in the European fossils, and also has additional characters which, taken together, are valuable clues in determining the ancestry of the Manidae.

ORDER **PHOLIDOTA** WEBER, 1904
FAMILY **MANIDAE** GRAY, 1821
PATRIOMANIS,[2] NEW GENUS

TYPE: *Patriomanis americanus*, new species.

DIAGNOSIS: Size about that of *Manis javanica* or *Manis pentadactyla* but with more distinct lambdoid crest and more sharply defined muscular crests on limb bones. Metapodials with distal keels developed only on ventral surface rather than continuing over distal end onto dorsal surface as in *Manis*. Profile of trochlea and distal border of entepicondyle both concave rather than convex as in *Necromanis*. Configuration of entepicondyle similar to most living manids but unlike *Manis temminckii* and *Teutomanis*, both of which have a more medially projecting, anteroposteriorly flattened entepicondyle with a proximodistally expanded medial end. Frontoparietal suture transverse rather than obliquely directed as in *Leptomanis*, which is not incontrovertibly a manid. Pectoral crest of humerus distally elongated to entepicondylar bridge and folded over medially which serves to distinguish it from dasypodids in which this crest extends about halfway down humerus and is directed instead toward ectepicondyle. Among

[1] In a paper published while the present paper was in press, von Koenigswald (1969) considered *Teutomanis* and "*Galliaetatus*" to be synonyms of *Necromanis*. He described a new species, *Necromanis parva*, from the early Burdigalian at Wintershof-West. The holotype is a distal fragment of a right humerus, and he designated as paratypes a right femur and left ulna from the same locality.

[2] From Latin *patria*, fatherland, native country, and *Manis*, the generic name of the living pangolin.

palaeanodonts and xenarthrans, only forms that have a cranium similar in shape to that of *Patriomanis* are myrmecophagids, but relationships of bones and particularly basicranial foramina are so different that they could not be easily confused.

DISTRIBUTION: Early Oligocene (Chadronian) of Natrona County, Wyoming.

Patriomanis americanus, new species
Figures 8–25

TYPE: F:A.M. No. 78999. Cranium, several vertebrae, part of left humerus, parts of both radii, part of right ulna, fragments of pelvis, shaft of right tibia, proximal end of left tibia, proximal end of right fibula, part of right calcaneum, three phalanges, and other fragments.[1]

LOCALITY AND STRATIGRAPHIC POSITION: From the badlands of the "White River" Formation at the head of the South Fork of Lone Tree Gulch, near the base of a prominent erosion scarp known locally as Flagstaff Rim. Approximately 5 miles north-northwest of the town of Alcova, in the E. ½ of sect. 27, T. 31 N., R. 83 W., Natrona County, Wyoming.

The specimen was collected from the surface at the level of volcanic ash "F," also known as the "375-foot ash." This terminology was used by the collectors because, in these deposits, this ash was preceded in deposition by five other distinct ash beds (A, B, C, D, and E) and, on a measured section used for zonation of specimens, ash F was 375 feet above the base. A Chadronian age of *Patriomanis* is confirmed by the associated assemblage of mammals. A middle Chadronian age was assigned to ash F by Evernden, Savage, Curtis, and James (1964), who computed the absolute ages from potassium-argon ratios. A sample of biotite from ash F gave an age of 33.7×10^6 years, and sanadine and feldspar from the same ash, a date of 35.7×10^6 years. The stratigraphic paleontology of these deposits will be the subject of another paper.

[1] During the summer of 1969, after the present report had been submitted for publication, more bones of a fossil pangolin were found about 10 feet above the ash F zone in the South Fork of Lone Tree Gulch. None of these bones duplicated any of those designated as the type specimen of *Patriomanis americanus*. Hopes that the newly found bones were part of the same individual were confirmed when I returned from the field and discovered six contacts between the newly found bones and those described. The additional remains to be included in the type specimen are: parts of several other vertebrae, parts of a scapula, parts of both humeri, part of the left ulna, carpals, two distal phalanges, a fragment of femur, distal end of left tibia, and tuber calcis of right calcaneum, as well as many other fragments, including ribs and vertebral processes. Following statements of the present report delimiting the preserved parts of *P. americanus* should be mentally emended to include the newly found parts. These were not prepared in time to be included in the present report, so additional information on them will be published later. No conclusions of the present study are altered by new information. None of these bones was found in place, but the highest was about 10 feet above ash F, and the small badland knob on which they were found does not extend more than 15 feet above ash F. The interval from which they were derived is therefore between 10 and 15 feet above ash F.

DESCRIPTION

In the following description, any reference to *Patriomanis* is to the type, *P. americanus*, F:A.M. No. 78999, the only specimen of this genus known at this time. Because *Patriomanis* is most like *Manis* among living genera, comparisons in this section are primarily between these two genera. Comparisons and contrasts with the European fossil forms, metacheiromyids, and xenarthrans are made in a later section of this report.

SKULL

The anterior portion of the skull of *Patriomanis* is broken away at the level of the cribriform plate, which is also missing. The cranium is similar in form to that of *Manis* or, among the xenarthrans, *Tamandua* (figs. 8A, 9A, 10A). Viewed from above it is barrel-shaped, slightly convex longitudinally, and evenly rounded transversely, with no sagittal crest to break the curve. There is very little postorbital constriction (which, if like *Manis*, would really be interorbital).

The sutures between the individual bones of the skull are distinct, although the epiphyses of the limbs were fused, indicating that the animal was mature. The frontoparietal suture is straight and extends transversely across the cranium at right angles to the median dorsal suture, which is also straight. In posterior view, the profile of the cranium is oval, wider than high. The lambdoid suture is slightly in advance of the lambdoid crest, so that a portion of the supraoccipital is exposed dorsally. A rather large triangular interparietal is present anterior to the supraoccipital, extending between the posterior

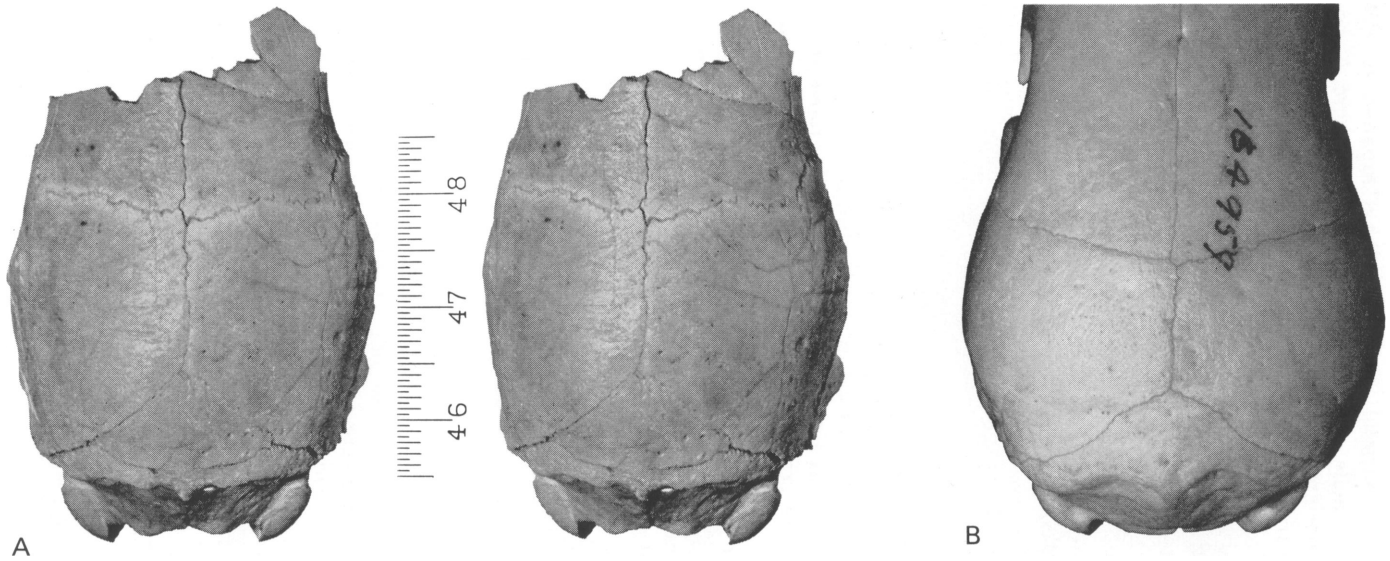

FIG. 8. Comparative views of cranii. A. *Patriomanis americanus*, cranium of type, F:A.M. No. 78999. Dorsal view. Stereo pair. B. *Manis pentadactyla*, cranium, A.M.N.H. (M.) No. 184959. Dorsal view. Sutures slightly emphasized. All approximately $\times 1.5$; scale divisions are 0.5 mm.

ends of the parietals. Parker (1885), in an embryological study of *Manis*, reported that there is no separate center of ossification and no bone that could be called an interparietal. This statement was difficult to reconcile with the presence of a separate interparietal in *Patriomanis* and what appears to be an interparietal in *Manis*. My conclusion that Parker's observation was incorrect was supported by a publication so recent that it was not available when the first draft of the present paper was written. Jollie (1968, pp. 277–278) observed that in a new-born *Manis javanica* interparietals were present, fused at the midline but still separated by a cartilaginous strip from the supraoccipital.

In *Patriomanis* the lambdoid crest is distinct but produced only posteriorly, not rising above the dorsal nor extending beyond the lateral edges of the cranium. Other muscular insertions can be seen anterior to this crest on the parietals and squamosals but these insertions are not produced into a crest. *Manis* shows this same feature. A small median vertical crest similar to that of *Manis* descends from the center of the lambdoid crest.

The occipital condyles are broad and protruded posteriorly. Their ovoid articular surfaces have narrow ventral extensions directed anteromedially but, because of breakage, it cannot be determined whether they met at the midline. Viewed from the posterior, the foramen magnum is large and uniformly oval, wider than high.

The squamosals of *Patriomanis* are exposed entirely on the lateral and ventrolateral surfaces of the cranium (figs. 9A and 10A); they cannot be seen when the cranium is viewed from above. The suture at the dorsal edge of these bones is straight and horizontal (parallel to the base of the skull). The zygomatic processes are small, directed downward and forward, and, although somewhat weathered, appear to have ended in a rather sharp point. There was apparently no glenoid articular surface. The lower jaw, although not preserved, must have been very reduced and probably contacted lightly with the ventromedial side of the zygomatic process as it does in *Manis*.

The basioccipital-basisphenoid tract is rather narrow and decreases in width anteriorly (fig. 9A). The suture between the two bones is closed but was apparently midway along the medial side of the otic region. The sphenoidal wings that extend the narial channel backward to the basioccipital in *Manis* were apparently also present in *Patriomanis*, but the ventral part has been broken away.

The tympanics of *Patriomanis* are not preserved, and there is no evidence of a bulla having been attached to any of the basicranial bones. The bulla probably consisted of a loosely attached, crescentic tympanic, as in most species of *Manis*, although we cannot rule out the possibility that an entotympanic was also present; van der Klaauw (1931, p. 269) observed a small, free bony entotympanic in both *Manis tricuspis* and *M. gigantea*.

The size and positions of all the basicranial foramina are remarkably similar to those of *Manis* (fig. 9). The condylar (hypoglossal) foramen is relatively large and is midway between the condyle and the otic cavity. The posterior lacerate foramen was evidently slightly anterolateral to the condylar foramen but its exact size and position cannot be accurately determined owing to the displacement of the petrosals. A groove that may have been either for the inferior petrosal sinus or the median entocarotid artery is medial to the posterior lacerate foramen, distinctly impressed into the basioccipital. This groove appears to lead forward from the condylar (hypoglossal) foramen but, if this is the case, either the function of the groove is misinterpreted or the foramen is misidentified. In *Manis gigantea* there is no separate condylar foramen; it has merged with the posterior lacerate foramen. This fact caused consideration of the possibility that the foramen of *Patriomanis* labeled CF (condylar foramen) in figure 9 is a common condylar-posterior lacerate foramen as in *M. gigantea*. This seems not to be the case, however, as the foramen in question is completely surrounded by the basioccipital bone. *Patriomanis* is apparently like *M. pentadactyla* as shown in the figure.

A foramen is present between the petrosal and basisphenoid along the medial side of the otic cavity. The inferior petrosal sinus probably passed through this foramen. Medially and anteriorly from this foramen is a narrow groove in the ventral surface of the basisphenoid. In some specimens of *Manis* a similar groove marks the position of the vidian branch of the seventh cranial nerve which was forced to assume this more posterior position because of the backward extension of the sphenoidal wings forming the narial channel. The median lacerate foramen

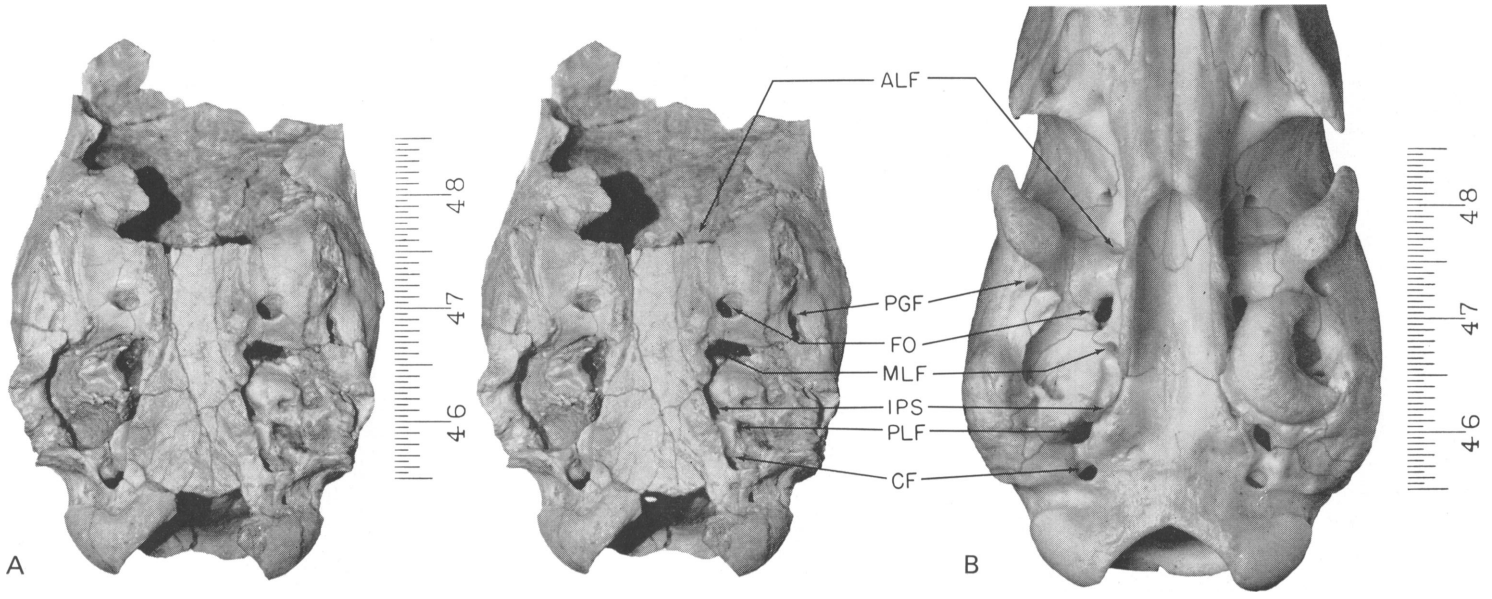

FIG. 9. Comparative views of cranii. A. *Patriomanis americanus*, cranium of type, F:A.M. No. 78999. Ventral view. Stereo pair. B. *Manis pentadactyla*, cranium, A.M.N.H. (M.) No. 184959. Ventral view. Sutures slightly emphasized. All approximately $\times 1.5$; scale divisions are 0.5 mm.

Abbreviations: ALF, anterior lacerate foramen; CF, condylar foramen = hypoglossal foramen; FO, foramen ovale; IPS, foramen for inferior petrosal sinus and vidian nerve; MLF, median lacerate foramen; PGF, postglenoid foramen; PLF, posterior lacerate foramen.

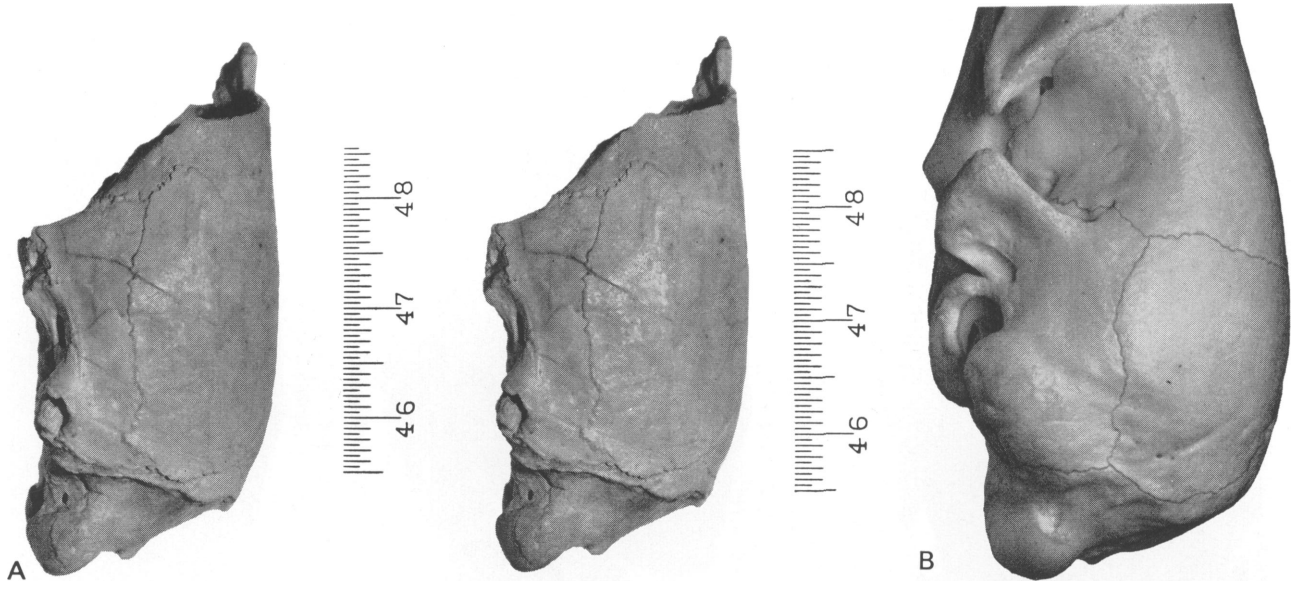

FIG. 10. Comparative views of cranii. A. *Patriomanis americanus*, cranium of type, F:A.M. No. 78999. Lateral view. Stereo pair. B. *Manis pentadactyla*, cranium, A.M.N.H. (M.) No. 184959. Lateral view. Sutures slightly emphasized. All approximately $\times 1.5$; scale divisions are 0.5 mm.

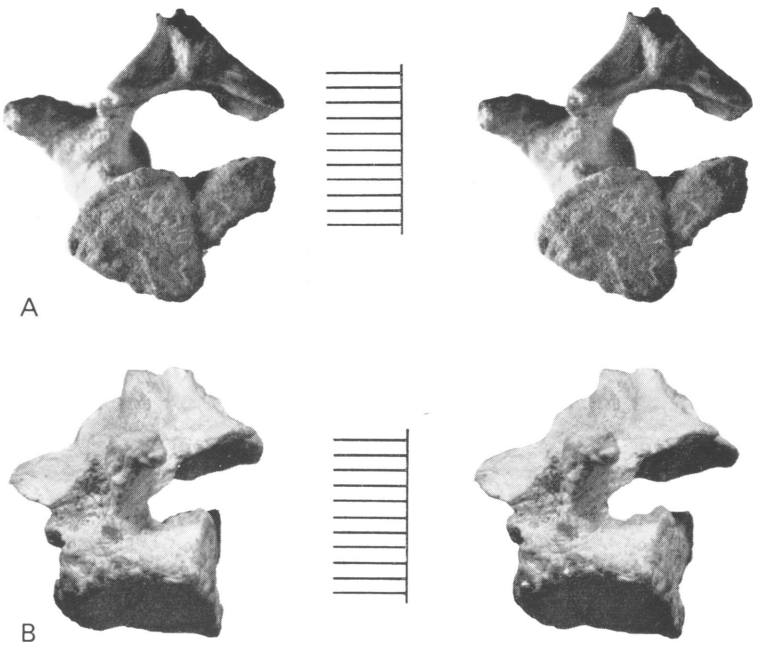

FIG. 11. *Patriomanis americanus*, part of cervical vertebra of type, F:A.M. No. 78999. A. Posterior view. Stereo pair. B. Left lateral view. Stereo pair. Approximately ×2; scales in mm.

was apparently a slit between the petrosal and alisphenoid, as in *Manis*, but the petrosals of *Patriomanis* are displaced so that the original size and position of this foramen cannot be accurately determined. The postglenoid foramen, foramen ovale, and anterior lacerate foramen are, in size and position, almost exactly as they are in *Manis* (fig. 9). The foramen rotundum is absent; the second branch of the trigeminal nerve probably passed through the anterior lacerate foramen as it does in *Manis*.

BRAIN

An endocranial cast of *Patriomanis* has been prepared from which can be determined the gross morphology of the brain. The petrosals are somewhat displaced, and it was not possible to prepare the cranial cavity well enough so that the details of the ventral side of the brain could be determined.

Of the olfactory bulbs, the only impression preserved is of the dorsal surface. These lobes were short, at the same level as the anterior end of the cerebral hemispheres, and had no fibers entering dorsally. *Manis* is similar in these respects.

The cerebral hemispheres are less inflated than those of *Manis*. Details of the upper surface are not well defined but the pattern of sulci seems to have been similar to that of *Manis*. What appears to be the rhinal fissure is only slightly higher than in *Manis*.

The midbrain is not exposed and, as noted above, detail is lost in this area.

A bony tentorium is present but this does not project between the cerebrum and cerebellum nearly as much as in *Manis*. The vermis and lateral lobes of the cerebellum are about equal in size, much as they are in *Manis*.

The cerebral hemispheres do not overlap the olfactory bulbs or the cerebellum, so that, in lateral view, the brain is seen to have a simple serial arrangement of the three major parts. The chief difference between the brain of *Patriomanis* and that of *Manis* is that in the latter the cerebral hemispheres are more inflated.

VERTEBRAE

In the type specimen of *Patriomanis americanus* only four reasonably complete vertebrae are preserved, but these, along with fragments and

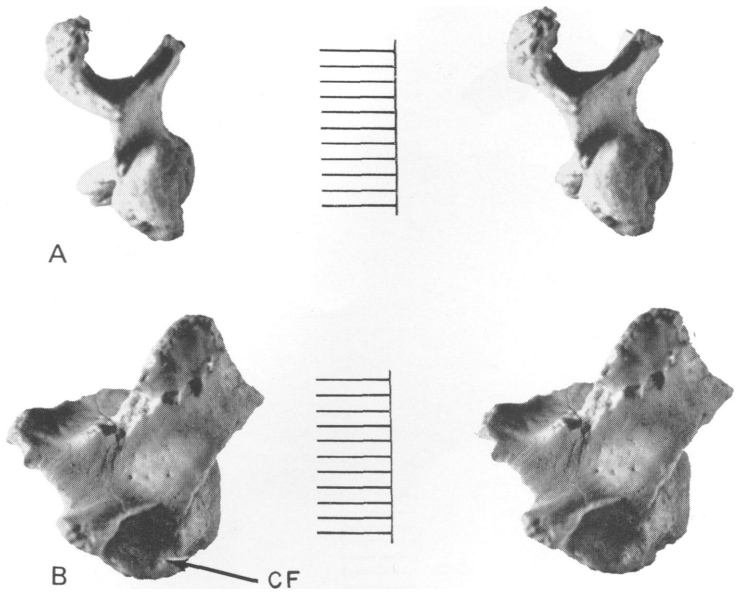

FIG. 12. *Patriomanis americanus*, right side of posterior thoracic vertebra of type, F:A.M. No. 78999, showing curved prezygapophysis. A. Anterior view. Stereo pair. B. Right lateral view. Stereo pair. CF, capitular facet. Approximately ×2; scales in mm.

processes of others, show much similarity to those of *Manis*.[1]

CERVICALS: Only one fragmentary cervical of *Patriomanis*, probably the sixth or seventh, is preserved (fig. 11). The centrum is broad, short, and depressed, with no ventral keel. The ventral surface is similar to that of *Manis* in that it has many small pits or foramina, giving it a spongy appearance. The arch is broad and low; the spine, which was slender with a triangular cross section, is broken away. The articular surfaces of the postzygapophyses are flat and almost horizontal, facing downward. Those of the prezygapophyses are slightly convex and inclined at about 45 degrees, so that they face outward and upward. Spinal nerves exited through deep notches in the posterior edge of the arch, beneath the postzygapophyses. These notches extend forward about half the length of the centrum, as they do in *Manis*.

DORSALS: Only one fragment can be definitely identified as part of a dorsal vertebra, and it is one of the most posterior. This fragment is particularly interesting because it shows that the "embracing" zygapophyses were as fully developed in *Patriomanis* as they are in *Manis*. In this fragment, the prezygapophysis is strongly concave, facing inward and downward (fig. 12). The postzygapophysis of the next vertebra was found in articulation and subsequently separated. This process is almost cylindrical with the articular surface facing outward and upward. The prezygapophysis had a dorsolaterally directed spine, which is now broken off. The capitular facet is also seen in this fragment. It is round, concave, slightly posterior to, and separated from, the anterior articular surface of the centrum (fig. 12B). The morphology of this fragment of dorsal vertebra of *Patriomanis* is virtually identical to the corresponding part of the last dorsal of *Manis*.

LUMBARS: Of the lumbars, only a fragment of one arch is preserved in *Patriomanis*. Little can be said of it other than that it also had the "embracing" zygapophyseal articulation.

SACRUM: Not preserved in *Patriomanis*.

CAUDALS: In *Patriomanis*, three centra of caudal vertebrae with parts of the arches are

[1]Parts of several other vertebrae of the same individual were collected in 1969 as noted in footnote on p. 466. These parts all agree with the following descriptions and even more strongly reinforce the following conclusions based on the "embracing" zygapophyses of the posterior dorsal and lumbar vertebrae.

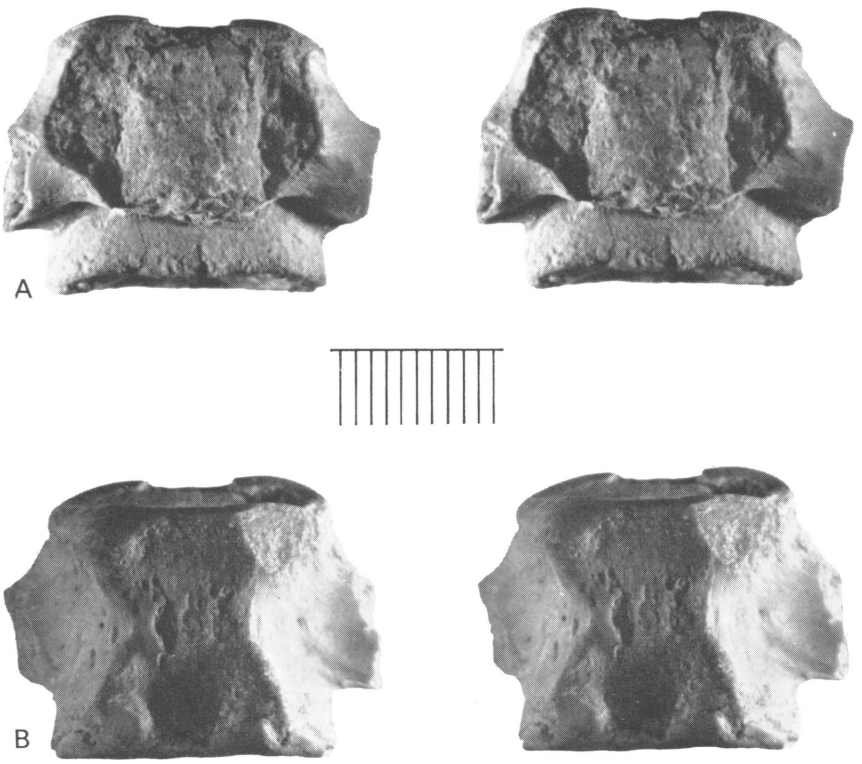

FIG. 13. *Patriomanis americanus*, centrum of anterior caudal vertebra of type, F:A.M. No. 78999. A. Dorsal view. Stereo pair. Anterior is toward top. B. Ventral view. Stereo pair. Approximately $\times 2$; scale in mm.

preserved, along with fragments of processes of several other caudals. The largest of the three centra was evidently from one of the most anterior caudals (fig. 13). At first it seems to be too large for an animal of this size, but when compared with those of *Manis*, it is not abnormal. The centrum is about as wide as long and dorsoventrally compressed, the articular facets oval, wider than high. It is slightly excavated below, with the articular facets for the chevrons at the bottom of short paired processes. The neural arch is not preserved. It can be seen that the spinal nerves exited through notches in the posterior edge of the arch. The bottom side of the centrum has the pitted, spongy texture like the caudals of *Manis*.

The other two centra (fig. 14), which were evidently from median caudals, are about twice as long as wide, with nearly circular articular surfaces. The ventral surfaces are excavated between paired longitudinal crests at the ends of which are the articular facets for the chevrons. The neural arches are low, with a short, transversely flattened spine. The zygapophyses are missing because of breakage but were probably functional. The transverse processes are also missing, but the broken section of them near the centrum shows that they were expanded anteroposteriorly into flat horizontal plates, probably similar to those in *Manis*.

Two transverse processes of other caudals are preserved. One of these is a broad, flat plate. The other is also flat, but longer and less anteroposteriorly expanded. It has a low crest for muscle attachment running diagonally across the upper surface and corresponds very closely to the transverse processes of the anterior caudals of *Manis*. None of the chevron bones of *Patriomanis* is preserved.

PECTORAL GIRDLE

None of the elements is preserved in *Patriomanis*.

FORELIMB

None of the bones of the forelimb is complete,

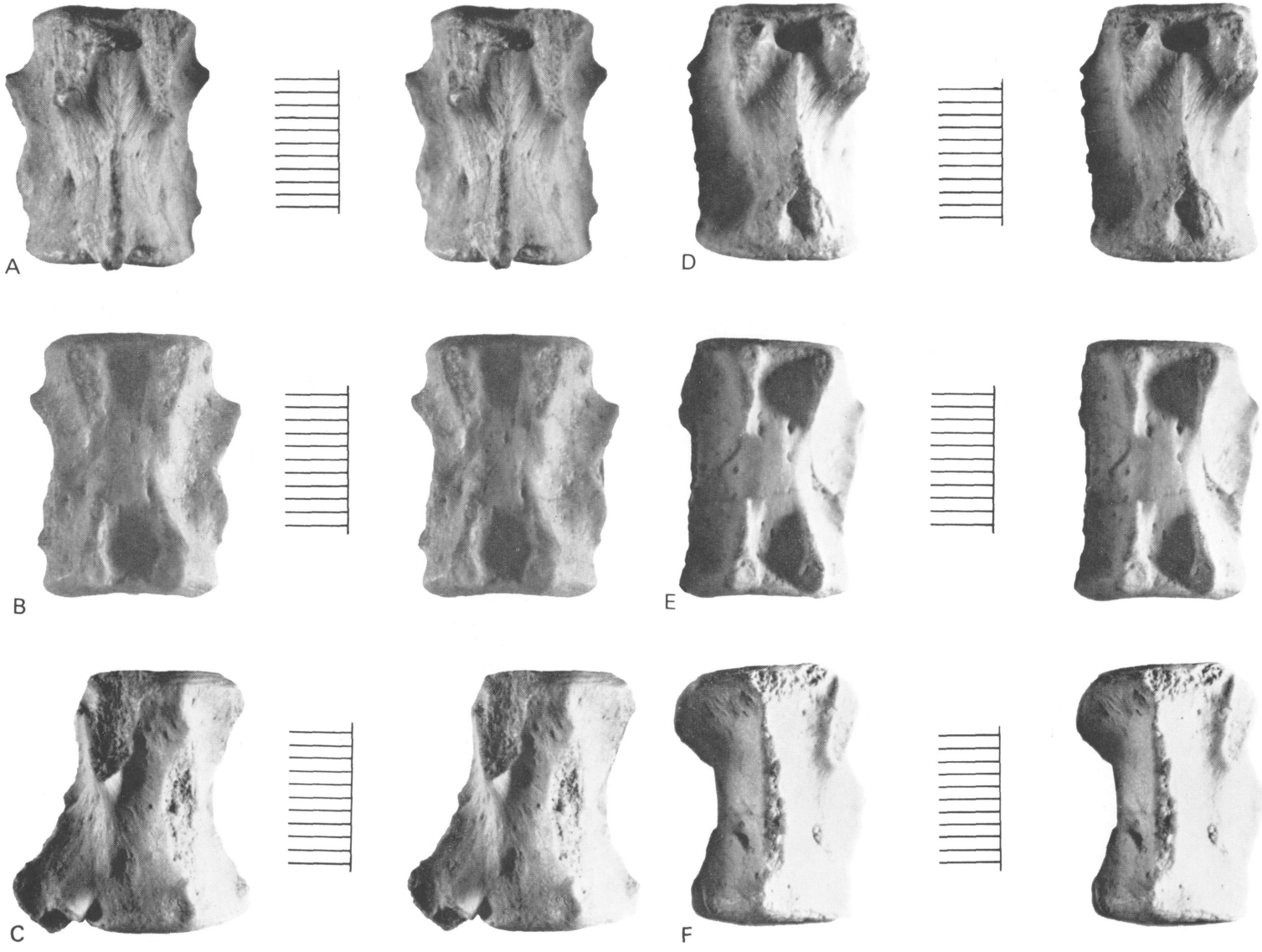

FIG. 14. *Patriomanis americanus*, two median caudal vertebrae of type, F:A.M. No. 78999. A. Dorsal view. Stereo pair. B. Ventral view. Stereo pair. Same as A. C. Right lateral view. Stereo pair. Same as A and B. D. Dorsal view, Stereo pair. E. Ventral view. Stereo pair. Same as D. F. Left lateral view. Stereo pair. Same as D and E. All approximately $\times 2$; scales in mm.

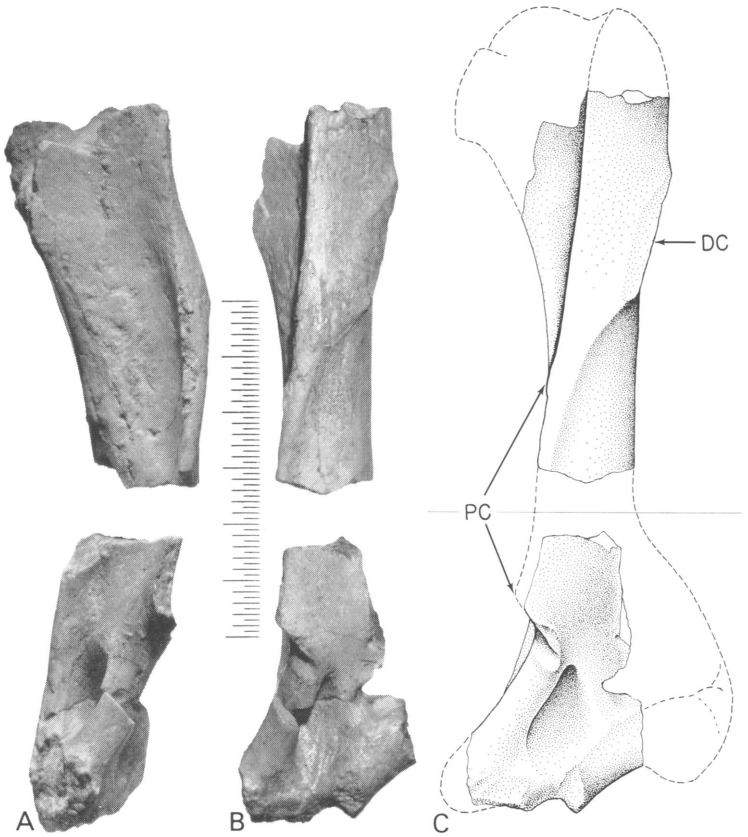

FIG. 15. *Patriomanis americanus*, parts of left humerus of type, F:A.M. No. 78999. A. Part of shaft and entepicondylar area with trochlea. Medial view. B. Same parts as A. Anterior view. C. Restoration based on parts seen in A and B. Anterior view. DC, deltoid crest; PC, pectoral crest. All approximately $\times 1.5$; scale divisions are 0.5 mm.

but parts of both humeri, parts of both radii, and part of the right ulna are present.[1]

HUMERUS: Of the right humerus, all that is present is the entepicondylar area with part of the trochlea. The left humerus is more complete, but unfortunately it lacks the proximal end, a short section of the shaft, and the lateral portion of the distal end. Enough remains, however, to show the distinctive manid characters (figs. 15 and 16). The bone is slightly arched forward; the delto-pectoral crest extends distally to the upper end of the entepicondylar bridge. In its proximal portion the crest is broad with a flat anterior surface, but the two borders of the crest merge distally to become a single crest (the pectoral crest), which is folded over medially so that it extends beyond the medial side of the shaft. The distal end of this crest ends abruptly at a well-defined groove through which passed the tendon of the biceps muscle. The posteromedial edge of the shaft also has a crest extending from the posterior edge of the entepicondyle presumably to the lesser tubercle. The belly of the biceps muscle lay along the medial side of the shaft in a trough formed between this latter crest and the delto-pectoral crest (fig. 15A). If the biceps inserted into the radius, it is obvious that it would have been sharply inflected where it passed around the distal end of the delto-pectoral crest and beneath the ventral edge of the pectoralis major muscle. With this limitation the biceps would tend to pull the radius medially

[1] As noted in footnote on p. 466, part of a scapula, additional parts of both humeri, and part of the left ulna of the same individual were found in 1969.

FIG. 16. *Patriomanis americanus*, parts of left humerus of type, F:A.M. No. 78999. These are the same bones as seen in figure 15 but are shown here in stereo view. Approximately $\times 2$; scales in mm.

rather than flexing it upward. But in *Manis*, and presumably in *Patriomanis*, this problem is more apparent than real, because Humphry (1870) and Windle and Parsons (1899) observed that the biceps of *Manis* is a simple muscle, single throughout its entire length, and inserts only into the ulna. With this more medial insertion, the tendon of the biceps can extend past the distal end of the pectoral crest with only a small amount of inflection.

In front view (figs. 15B, 15C, and 16), the profile of the trochlea of *Patriomanis* is slightly concave as it is in some species of *Manis* (e.g., *M. pentadactyla* and *M. javanica*). The entepicondylar bridge has the same relationships as in *Manis*, merging distally with the anterior surface of the entepicondyle. The capitulum is missing in both humeri of *Patriomanis*, but the smoothly concave capitular surface of the radius indicates that the capitulum was spherical and unkeeled

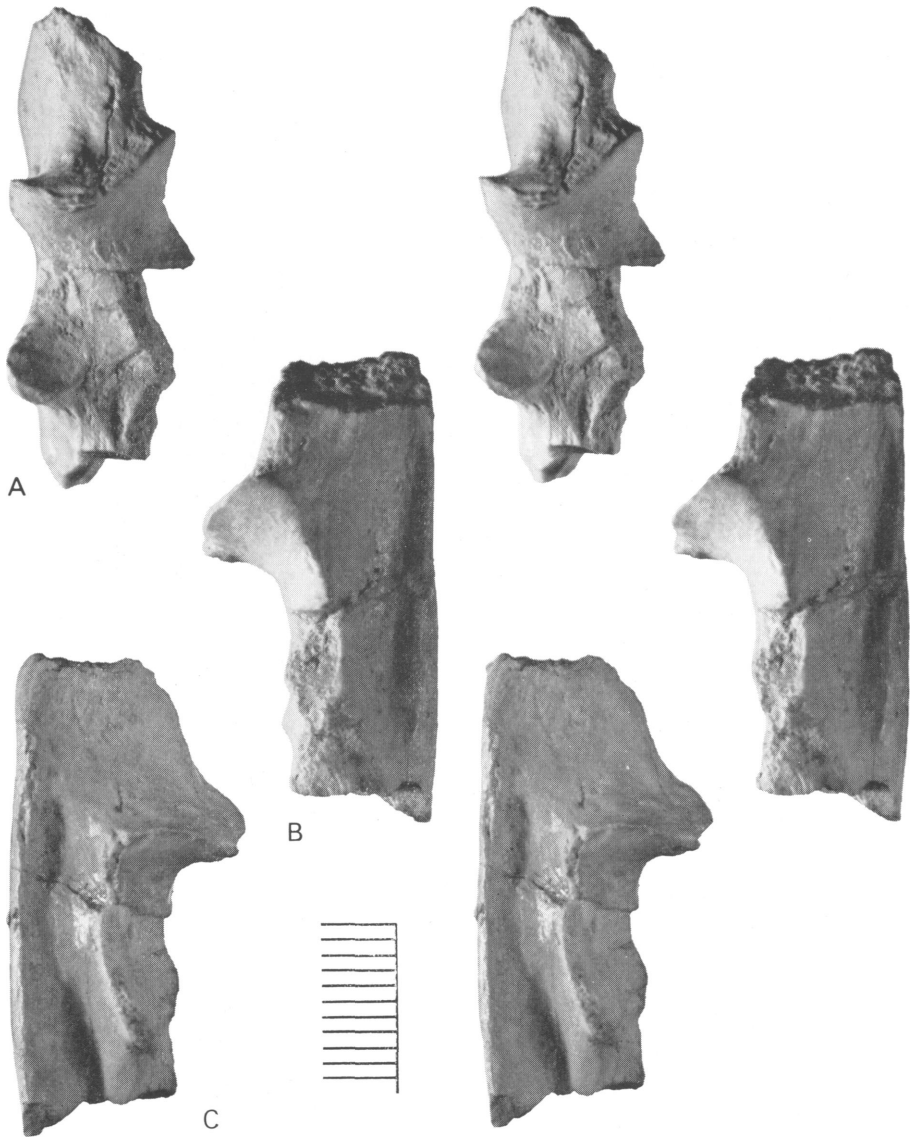

FIG. 17. *Patriomanis americanus*, proximal part of right ulna of type, F:A.M. No. 78999. A. Anterior view. Stereo pair. B. Medial view. Stereo pair. C. Lateral view. Stereo pair. All approximately ×2; scale in mm.

as it is in *Manis*.[1] The details of the ectepicondyle and supinator crest are unknown but it can be seen that the proximal part of this crest curved back to merge with the posterior side of the shaft as it does in *Manis*. On the posterior side of the humerus, just above the trochlear articular surface, is a deep, transversely oval depression for the reception of the elevated superior margin of the semilunar notch of the ulna.

The humerus of *Patriomanis* differs from that of *Manis* in its more angular appearance, because of the stronger development of muscular crests, although in *Manis gigantea* the crests are

[1]This inference was confirmed by the capitulum of the right humerus which was with the additional remains discovered in 1969 as noted in footnote on p. 466. This capitulum contacts the trochlea and entepicondylar area that had been previously found and noted above.

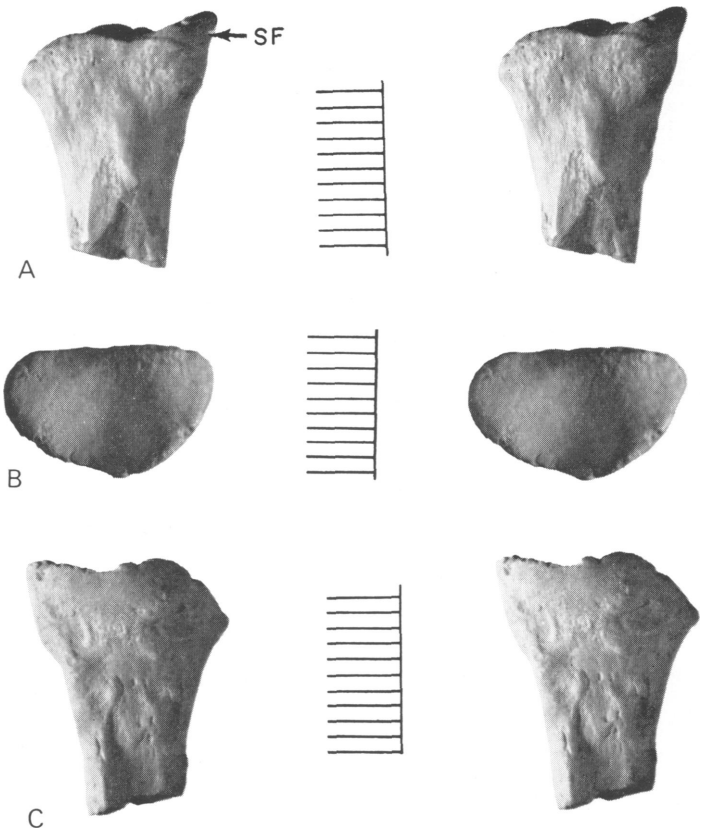

FIG. 18. *Patriomanis americanus*, proximal part of left radius of type, F:A.M. No. 78999. A. Anterior view. Stereo pair. SF, "sesamoid" facet described in text. B. Proximal view. Stereo pair. Anterior is toward top. C. Posterior view. Stereo pair. All approximately $\times 2$; scales in mm.

nearly as strong and sharp as in *Patriomanis*. In this respect *Patriomanis* is more similar to *Teutomanis* and *Necromanis*.

ULNA: In *Patriomanis*, only a part of the right ulna is present, including the semilunar notch, part of the olecranon process, and the proximal part of the shaft (fig. 17). There is some indication that the olecranon had a slight inward twist. The sides of the shaft are excavated between the semilunar notch and the flat posterior border. The semilunar notch is transversely expanded with an elevated superior margin (anconaeal process). The humeral and radial surfaces are contiguous, but distinct from one another. On the anterior surface, just distal to the semilunar notch and toward the lateral side of the shaft, is a small rugose process, presumably for the insertion of the biceps. This ulna is very similar to that of *Manis*.

RADIUS: The proximal end of the left radius and the distal ends of both radii are present. The proximal end is more transversely expanded than that of *Manis* (fig. 18); it is quite similar, as far as can be judged from the figures, to that described and figured by Helbing (1938). The proximal end has three confluent articular surfaces: a cuplike capitular surface, a shelf lateral to this, and a medial trochlear extension. Posteriorly there is a small convex ulnar surface. At the lateral side of the proximal end is a small articular surface, similar to that in *Manis*, but smaller (fig. 18A). In *Manis* there is a "sesamoid" bone in the tendon of origin of the supinator brevis muscle. A concave facet of this "sesamoid" bone is applied to the small lateral articular surface of the proximal end of the radius. Another facet of this "sesamoid" is applied to the narrow flange of the articular

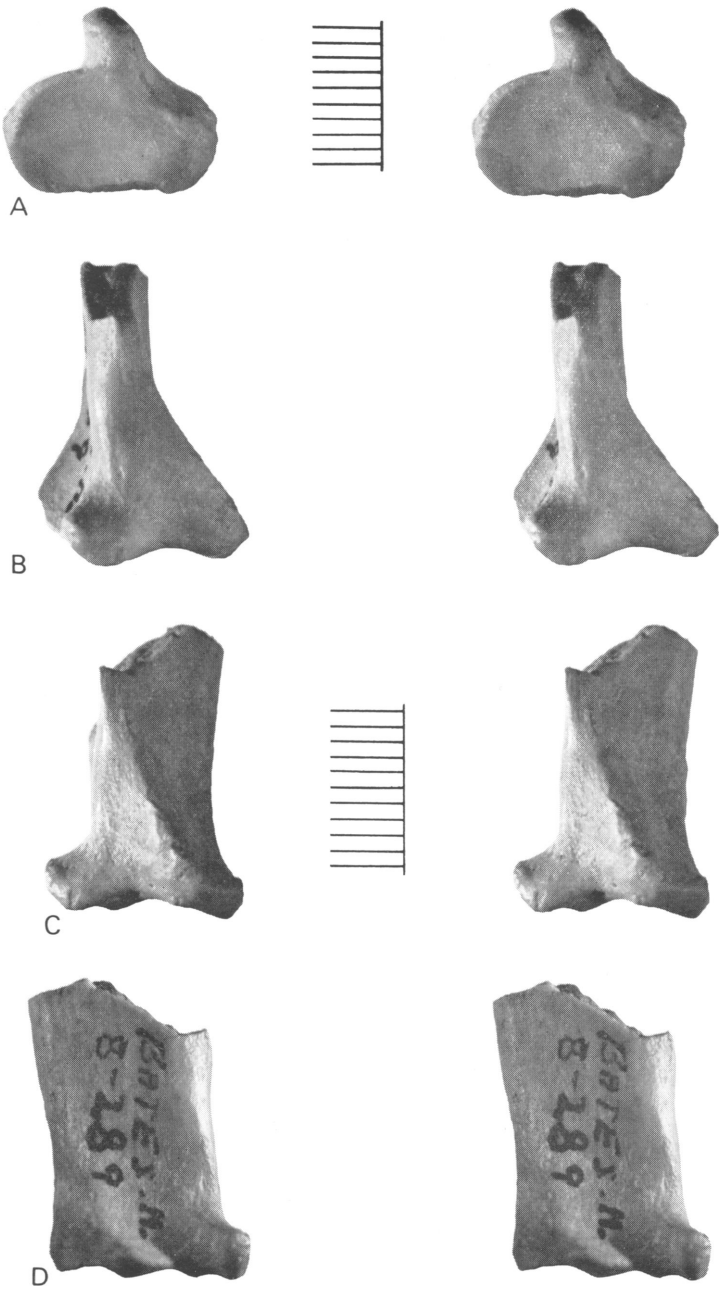

FIG. 19. *Patriomanis americanus*, distal end of right radius of type, F:A.M. No. 78999. A. Distal view. Stereo pair. B. Anterior view. Stereo pair. C. Medial view. Stereo pair. D. Lateral view. Stereo pair. All approximately $\times 2$; scales in mm.

surface of the humerus, lateral to the capitulum. *Patriomanis* apparently also had this "sesamoid" bone, although it may have been relatively smaller than that of *Manis*. The radius described and figured by Helbing (1938) also had this "sesamoid" articular surface; it clearly shows in the figure (fig. 5).

In *Patriomanis* the shaft of the radius, in its

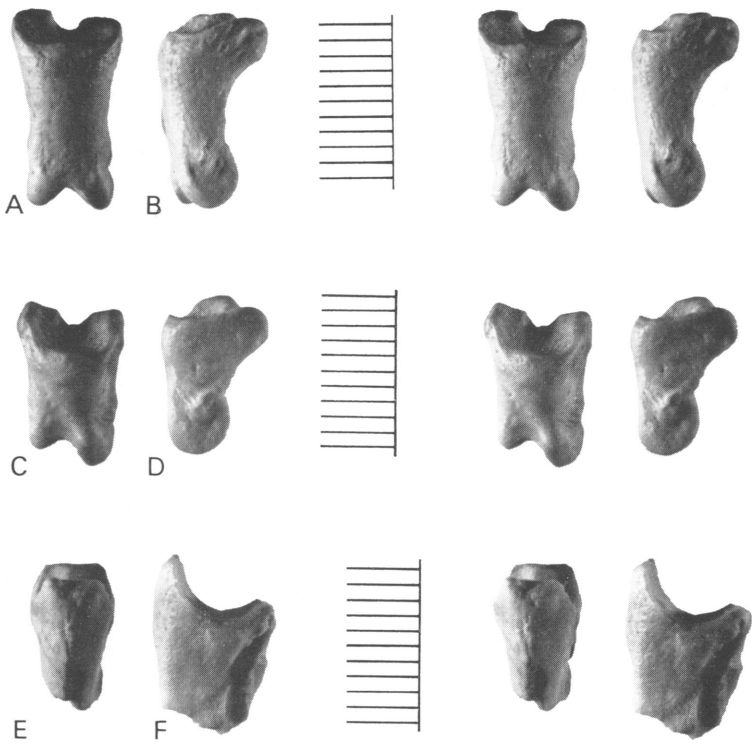

FIG. 20. *Patriomanis americanus*, phalanges of type, F:A.M. No. 78999. A. Proximal phalanx. Dorsal view. Stereo pair. B. Same as A. Lateral view. Stereo pair. C. Proximal phalanx. Dorsal view. Stereo pair. D. Same as C. Lateral view. Stereo pair. E. Distal phalanx. Dorsal view. Stereo pair. F. Same as E. Lateral view. Stereo pair. All approximately $\times 2$; scales in mm.

proximal portion, is quite slender and oval in cross section (fig. 18). The distal portion of the shaft is transversely flattened and expanded anteroposteriorly (fig. 19). The distal end is strongly expanded and heavy. It has a single concave, transversely oval articular surface for the scaphoid and lunar (fig. 19A). These two carpals are not known in *Patriomanis* so it cannot be determined if they were fused as they are in *Manis*. If they were not fused, they evidently had very little independent movement. The anterior crest of the radius is well developed and near the distal end it gives rise to a small anteriorly directed tubercle (fig. 19).

The radius of *Patriomanis* is unlike that of *Manis* in several features. In these same features it is more like a radius from the Miocene of Europe (fig. 5), described by Helbing (1938).

MANUS: In *Patriomanis* none of the metacarpals is present. Two proximal phalanges are present, however (fig. 20A–D), which allow the inference that the metapodials were keeled only on the ventral surface (or posterior surface, depending on the orientation), as the phalanges are grooved only near the ventral side of the proximal articular surface. The metapodials would therefore be more like those of *Teutomanis*. It will be recalled that Ameghino (1905) referred the metapodials of *Teutomanis* to a new genus, "*Galliaetatus*," because they did not have the specialized *Manis*-like keels, and he believed they were of an armadillo. But here again, in *Patriomanis*, is an animal with limbs showing most of the specializations of *Manis* but with feet more primitive. This is additional evidence that *Teutomanis* and "*Galliaetatus*" are synonymous.

The one distal phalanx (fig. 20E, F) of *Patriomanis* is lacking the tip but appears to have had a shallow fissure, which, if this is the case, is not

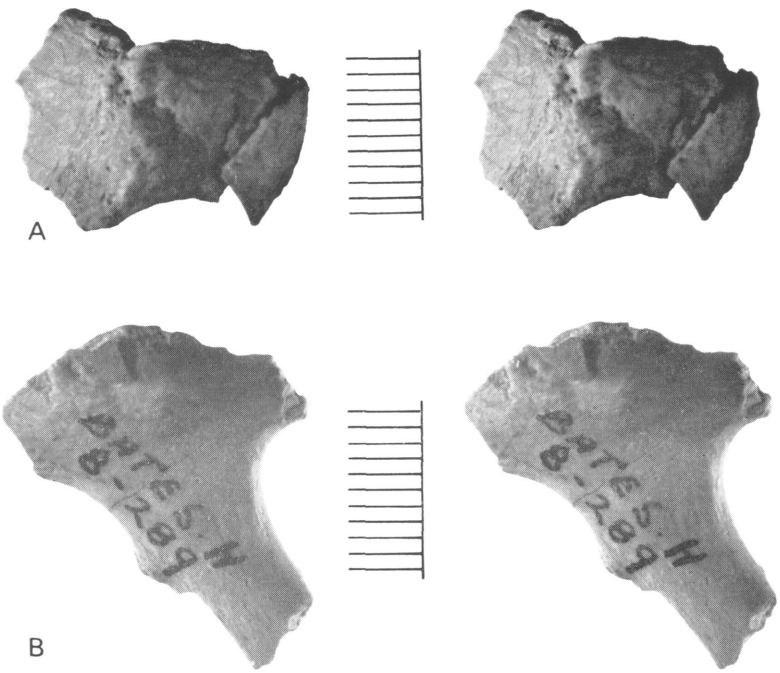

FIG. 21. *Patriomanis americanus*, parts of pelvis of type, F:A.M. No. 78999. A. Pubic symphysis. Ventral view. Stereo pair. B. Part of left acetabulum and upper part of shaft of pubis. Lateral view. Stereo pair. All approximately $\times 2$; scales in mm. Compare with figure 29.

so deep as it is in *Manis*.[1] The articular surface is relatively large and strongly curved with a median ridge separating the surface into two parallel grooves. This distal phalanx is probably from the third digit of one of the front feet. It is smaller than the same bone of *Manis gigantea*, but otherwise virtually identical, even to details of vascular foramina and sulci.

PELVIC GIRDLE

In *Patriomanis* only two fragments of pelvis are preserved: the pubic symphysis (fig. 21A) and a fragment of the right acetabulum with the upper portion of the shaft of the pubis (fig. 21B). The pubis descends from beneath the ventral part of the acetabulum, not quite so far posteriorly as it does in *Manis*. The upper portion of the shaft is a slender bar. Along the ventral border beneath the acetabulum are two small rugose processes, presumably for attachment of the psoas parvus musculature. The pubic symphysis is short with a small separate median triangular ossification, much as in *Manis* and many other mammals.

HIND LIMB

FEMUR: Not preserved in *Patriomanis*.

TIBIA: Most of the details of the tibia of *Patriomanis* can be determined except for the distal extremity.[2] The proximal end and a distal portion of the left tibia are present. Most of the shaft of the right tibia is present, but both extremities are lacking (figs. 22 and 23).

The proximal end is transversely expanded as in *Manis* (fig. 22A). The median condylar surface is slightly convex and continues up onto the side of the rather sharp intercondyloid spine. The lateral condylar surface is more strongly convex. Posteromedially the median condylar surface is confluent with, but separated by a low crest from, a small triangular articular surface that continues down onto the posterior side of

[1]Two complete distal phalanges were among the additional remains of the same individual discovered in 1969 as noted in footnote on p. 466. Both these phalanges are quite deeply fissured and are very similar to those of *Manis*.

[2]As noted in footnote on p. 466, the distal end of the left tibia of the same individual was collected in 1969.

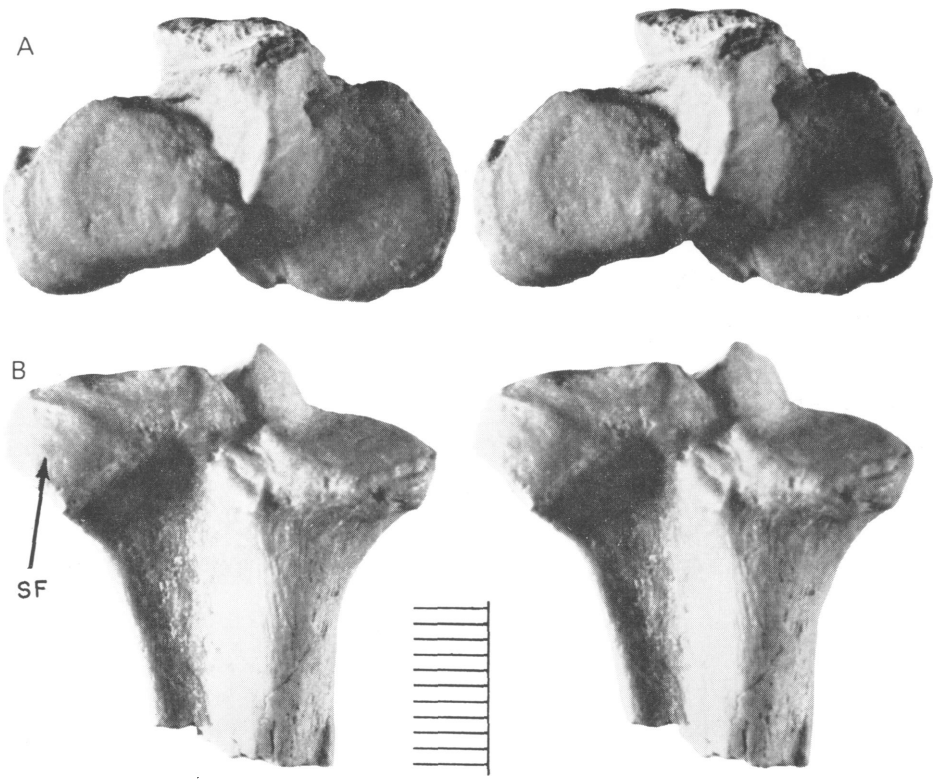

FIG. 22. *Patriomanis americanus*, proximal part of left tibia of type, F:A.M. No. 78999. See also figure 23. A. Proximal view. Stereo pair. B. Posterior view. Stereo pair. SF, "sesamoid" facet described in text. All approximately $\times 2$; scale in mm.

the bone (fig. 22B). In *Manis* the popliteus muscle has an ossicle in its tendon, which is applied to a similar downward extension of the lateral condylar surface of the tibia. *Patriomanis* certainly also had this "sesamoid."

The cnemial crest of the tibia of *Patriomanis* is very prominent and turned a bit laterally in its proximal portion (fig. 23). The crest extends farther down the shaft than it does in *Manis*. In the proximal part, the lateral surface of the shaft is excavated between the cnemial crest and another sharp crest that descends from beneath the fibular facet. The posterior surface of the shaft is concave beneath the lateral condyle and convex beneath the median condyle. Anteromedially the shaft is convex. The middle part of the shaft is more laterally compressed than in *Manis* (fig. 23).

The proximal articulation of the tibia of *Patriomanis* is much like that of *Manis*, but the muscular crests are sharper and the shaft more laterally compressed than in most of the living manids. Of the living species, *M. aurita* is most like *Patriomanis* in features of the tibia.

FIBULA: In *Patriomanis*, only the proximal end of the right fibula is preserved. This end is laterally flattened and anteroposteriorly elongated, with the tibial facet at the top of an anterior extension (fig. 24). Where broken, the shaft is very thin with no indication of having been curved.

PES: None of the elements is preserved in *Patriomanis* except for part of the right calcaneum (fig. 25). This bone is lacking the tuber calcis and part of the anteroexternal end.[1] It is unlike that of *Manis* in most respects, but closely approximates that of *Teutomanis* (fig. 32C) as nearly as can be determined from the figures. It is also much like that described by Helbing

[1]Additional remains of the same individual, collected in 1969 as noted in footnote on p. 466, include the tuber calcis that contacts the fragment of calcaneum described here. This additional part gives the calcaneum much the same shape as that of *Teutomanis* seen in figure 32C.

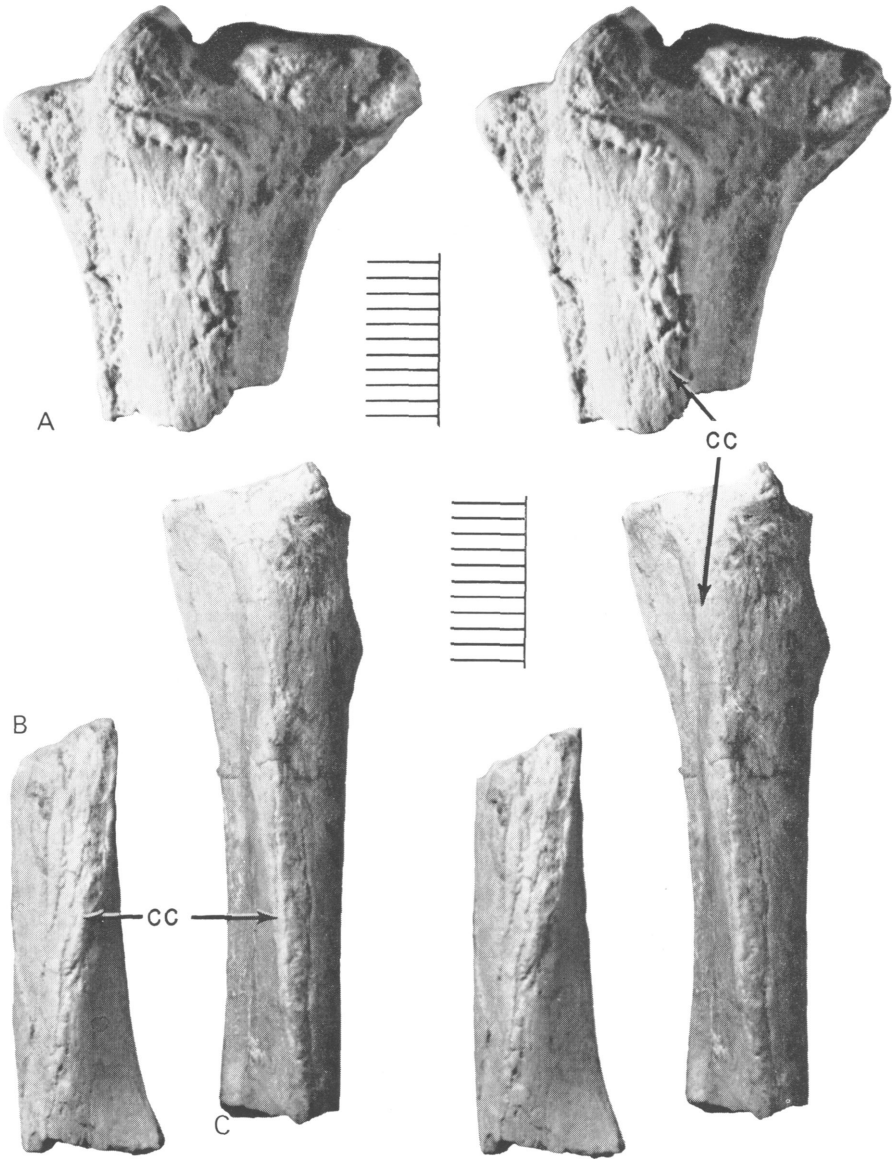

FIG. 23. *Patriomanis americanus*, parts of tibiae of type, F:A.M. No. 78999. A. Anterior view of proximal end of left tibia. Same as seen in figure 22. Stereo pair. CC, cnemial crest. B. Part of shaft of left tibia. Anterior view. Stereo pair. C. Part of shaft of right tibia. Anterior view. Stereo pair. All approximately $\times 2$; scales in mm.

(1938), which was also referred to *Teutomanis* (fig. 7).

MEASUREMENTS

Because most of the bones of the type specimen of *Patriomanis americanus* are incomplete, it is difficult or impossible to obtain any measurements that are presently useful. Nevertheless, the following measurements are included in the hope that any potential they may have may eventually be realized. All measurements are in millimeters.

Skull:

Maximum width of cranium	33.5
Width across condyles	22.6

FIG. 24. *Patriomanis americanus*, proximal end of right fibula of type, F:A.M. No. 78999. Lateral view. Stereo pair. Approximately ×2; scale in mm.

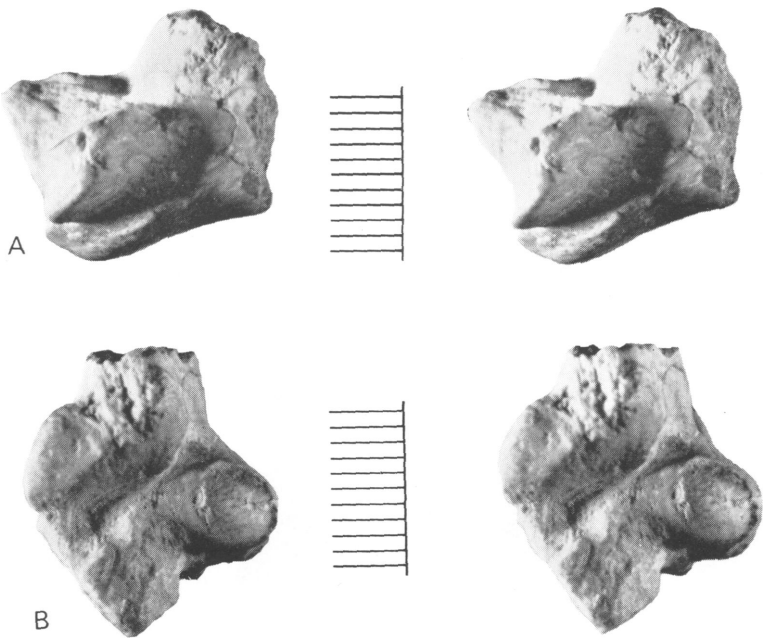

FIG. 25. *Patriomanis americanus*, part of right calcaneum of type, F:A.M. No. 78999. Compare with figures 7 and 31. A. Medial view. Stereo pair. B. Anterior view. Stereo pair. Approximately ×2; scales in mm.

Ulna:
- Total length of preserved part (fig. 17) . . 30.5

Humerus:
- Total length of upper part of shaft along anterior border (figs. 15 and 16) . . . 33.8

Radius:
- Transverse diameter of proximal end (fig. 18) 12.8
- Anteroposterior diameter of proximal end (fig. 18) 7.3
- Transverse diameter of distal end (fig. 19) 13.2
- Anteroposterior diameter of distal end, including tubercle (fig. 19) 12.2

Tibia:
- Maximum width of proximal end (fig. 22). 26.3

SUMMARY

Patriomanis has a more distinct lambdoid crest but is otherwise much like *Manis* in characters of the cranium. The vertebrae of *Patriomanis* were

like those of *Manis*, even to the "embracing" zygapophyses of the posterior dorsals and lumbars. The limb elements show most of the specializations seen in *Manis*, but the muscular crests are more strongly developed than in some of the living species of *Manis*. The metapodial-phalangeal articulations lacked the strongly developed keels seen in *Manis*. In these articulations, as well as in features of the humerus, radius, ulna, and calcaneum, *Patriomanis* was apparently quite similar to *Teutomanis*. Other comparisons are limited because of the scarcity of remains of the European genus. As shown in a following section, *Patriomanis* also has many points of resemblance to the metacheiromyids, as do the living pangolins. *Patriomanis* is relatively more similar to *Manis* than to any known North American forms.

PANGOLIN ANCESTORS

FOSSILS REFERABLE to the family Manidae can be traced as far back as the early Oligocene, at which time they are known from both Europe and North America. Because one of the earliest known manids is from North America, we can now consider the possibility that this continent may have been the original home of the family and look among its early Tertiary fossils for possible ancestors of the manids. Of the North American fossils, the only group ever seriously considered to be ancestral to the manids was the Palaeanodonta, more specifically the Metacheiromyidae. This idea was put forth by Matthew in 1918, but apparently received little support, primarily due perhaps to geographic inhibition; no pangolins were known from the New World and no palaeanodonts were known from the Old World. This geographic inhibition has now been overcome by the occurrence of a pangolin in the early Oligocene of North America. Matthew's idea was repudiated by Simpson in 1931 and has not received favorable comment, at least in print, since that time.

The palaeanodonts were first known from *Metacheiromys marshi*, which, as the name suggests, was described as a primate by Wortman (1903), who considered it to be closely related to the living aye-aye, *Daubentonia* Geoffroy, 1795 (=*Cheiromys* Cuvier, 1800). The material on which Wortman's genus was based was a composite of the bones of *Metacheiromys* and one of the true Bridgerian primates.

Osborn, in 1904, published a brief account of two new specimens, named them *Metacheiromys dasypus* and *M. tatusia*, and placed the genus among the Loricata. His interpretation of the osteology and affinities of *Metacheiromys* was summed up in the following paragraph:

"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 the ulna, elongation of the delto-pectoral crest of humerus. Still more widely specialized in the dentition, which is practically abortive except the tusk-like upper and lower canines which are covered with enamel. These at first sight suggest the tusks of the sloth *Choloepus*, 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 vertebrae and the presence of ossicles in the dermal shield to be described as a fully developed armadillo" (Osborn, 1904, p. 165).

There is no indication that Osborn compared *Metacheiromys* with *Manis*. Had he done so, it would surely have been apparent to him that the general osteology of these two genera is also very similar. The characters of *Metacheiromys* that he considered to be more primitive than those of the armadillos are not more primitive than those of *Manis*. And perhaps more important, the characters that he considered to be more specialized than in armadillos are not more specialized than they are in *Manis*. Even the addition of "compound articulations of the dorsal vertebrae" and "ossicles in the dermal shield" would still leave *Metacheiromys* far from a "fully developed armadillo."

Ameghino (1905) reserved judgment as to the affinities of *Metacheiromys*, but recognized features that he considered to be quite extraordinary for a primitive edentate, and suggested affinities with "*Galliaetatus*" (=*Teutomanis*). Matthew (1918, p. 620) considered this to be a "rather shrewd guess," not far from the conclusions he had reached in his study of *Palaeanodon*.

Scott (1913, pp. 616–617) was also reserved about the edentate affinities of *Metacheiromys*, concluding that, "While these curious animals may very possibly have been referable to the Edentata and, at all events, have several features suggestive of relationships to that order, it can hardly be maintained that they were unequivocal members of it."

Winge (1915, p. 307), in his study of the edentates of Lagoa Santa, concluded that *Metacheiromys* probably had nothing to do with the edentates. Even when Matthew's description of *Palaeanodon* was available to him, Winge (1923, pp. 343–344) still strongly opposed Osborn's and Matthew's beliefs in a palaeanodont-xenarthran relationship.

In 1918, Matthew described another genus, *Palaeanodon*, which is very closely related to, and

almost certainly the ancestor of, *Metacheiromys*. Intermediate forms are known. The ancestor-descendant relationship has never been questioned and has recently been reinforced by the description of the anterior part of a skull of a new species, *Palaeanodon woodi*, by Guthrie (1967). This specimen has large canines similar to those of *Metacheiromys*.

Matthew's study of *Palaeanodon* led him to conclude that it was related to the Xenarthra, but even more closely related to the pangolins. Citing what he considered to be intermediate stages in the European fossil manids, he concluded that the palaeanodonts were ancestral to the pangolins, and on his phylogenetic diagram (1918, p. 656) showed that the manids were derived directly from the genus *Palaeanodon*.

Matthew was a bit more conservative than Osborn in his conclusions regarding palaeanodont-xenarthran relationships. For "geographic and faunal reasons" he did not think *Palaeanodon* was directly ancestral to the Xenarthra, even though he found no structural difficulties in the way. Of *Metacheiromys*, Matthew (1918, p. 620) stated that, "It is convenient to rank it for the present in a distinct suborder, whose relationships to the Loricata are, I suspect, much like those of the creodonts to the fissipede Carnivora. The only family at present is the Metacheiromyidae, which, like the hyaenodonts, oxyaenids or mesonychids among the creodonts, 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."

When Matthew studied *Palaeanodon*, the pre-Santa Cruz edentates were practically unknown. With this lack of information he could speculate then (1918, p. 653) that, "I see no reason to believe that the lower Eocene and Paleocene ancestors of the Xenarthra were any more specialized than is *Palaeanodon* and I believe that they were quite closely related to it." With more recent evidence, however, we can see that Matthew incorrectly presaged what early Eocene and Paleocene armadillos were like. Paleocene armadillos are even yet not well known, but the early Eocene armadillo *Utaetus* was already much closer morphologically to recent armadillos than to palaeanodonts.

Abel (1922, pp. 291–293) accepted Osborn's and Matthew's views on palaeanodont-xenarthran relationships, but Schlosser (1923, p. 505) found it difficult to reconcile the remains of *Metacheiromys* with a carapace-less dasypodid. As noted before, Winge (1923) still remained firm in his conviction that the palaeanodonts and xenarthrans had nothing to do with one another. So, there were still some paleontologists who were not convinced.

In 1931, Simpson published a definitive and detailed comparative description of *Metacheiromys* in which he argued strongly in favor of Osborn's and Matthew's views of a palaeanodont-xenarthran relationship. But, unlike Matthew, he concluded that there was little evidence for the palaeanodont-manid relationship. He considered Matthew's (1918) argument but then dismissed the evidence seen in the European Tertiary manid remains stating (1931, p. 374) that, "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," and (p. 375), "It seems that the palaeanodonts 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 paleontological support." Simpson later (1945, p. 195) remarked that there was "little doubt that Pholidota do occur in the European mid-Tertiary," but he still did not acknowledge the palaeanodont similarities.

Simpson's conclusions regarding palaeanodont-xenarthran relationships were essentially the same as those of Matthew; Simpson emphasized at several points that the palaeanodonts were not directly ancestral to the Xenarthra but rather "that the relationship was collateral to the Xenarthra as a whole and not specifically to the armadillos." He realized that the palaeanodonts and xenarthrans could be related only through a common ancestor which he postulated to have lived in the early Paleocene or late Cretaceous.

Palaeanodont Characters and Comparisons

The discussion on the previous pages has covered in a general way the history of study of the palaeanodonts, and has pointed out the various authors' views on affinities of these fossil forms. Palaeanodonts have been variously considered as directly ancestral to the Xenarthra, directly ancestral to manids and related collaterally to the Xenarthra, and related collaterally

only to the Xenarthra but not at all to the Manidae. Other workers have denied that there was any relationship between Xenarthra and Palaeanodonta. Simpson's (1945) classification of the palaeanodonts in the Edentata has apparently been accepted by later workers.

With the discovery of a pangolin in North America, the palaeanodonts must once more be evaluated as candidates for the ancestry of the Manidae; the evidence must be reviewed. To anticipate, the conclusions of the present study are that the palaeanodonts are ancestral to manids and probably not closely or at all related to the Xenarthra. Because the transfer of the Palaeanodonta from the Edentata to the Pholidota reflects a major change in concepts of mammalian history as well as in classification, it should be given the formality of a thorough discussion of palaeanodont morphology and reasons for the change.

In his conclusions regarding relationships of *Metacheiromys* to the Xenarthra, Simpson (1931, pp. 368–371) systematically recapitulated the evidence in a series of 20 numbered statements. In the following discussion these statements are quoted and each is followed by a discussion and analysis of the evidence.

"1. The dentition [of *Metacheiromys*] is edentate-like in its tendency toward reduction and 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 reduction of the cheek teeth, which has gone further than in most later forms" (Simpson, 1931, p. 368).

That the dentition of the palaeanodonts is reduced and degenerate is not in itself any indication of relationship to the Xenarthra, and, although the ancestors of the Xenarthra in all probability had enamel on the teeth, the presence of enamel on the canines of the palaeanodonts does not imply that they are ancestral to the Xenarthra. In fact, the palaeanodonts are excluded from the direct ancestry of the Xenarthra not only because they appear too late in the record, but also because of the "prematurely specialized" reduction of the cheek teeth. This argument does not apply with the same force to the manids.

Matthew (1918, p. 654) wrote that, "The cheek teeth are evidently degenerating in the Metacheiromyidae; in *Manis* they have disappeared; in the lower jaw of the pangolin there is a bony process very suggestive in character and position of a vestigial remnant of the lower canine tusk of the Metacheiromyidae." This bony process, while perhaps serving a similar function, could hardly be considered a vestige of a tooth. However, Röse (1892) observed the presence of a single tooth anlage near the anterior end of each of the lower jaws of a 7.6 cm. fetus of *Manis tricuspis* and in both upper and lower jaws of a 9 cm. fetus of *M. javanica*. Starck (1940) also reported the presence of tooth anlagen in an embryo of *Manis javanica*. He found none in the lower jaws but two in the right upper jaw and three in the left upper jaw. These anlagen are separated by relatively large spaces from each other but are yet all near the anterior end of the jaws. The anterior position and reduced number of these tooth anlagen suggest that the ancestor of *Manis* was an animal with only a few teeth remaining near the anterior ends of the jaws. The palaeanodonts, particularly *Metacheiromys*, show this condition. The single anlage at the anterior end of both upper and lower jaws, found by Röse, may be vestiges of the large canines of the palaeanodonts.

Matthew (1918, p. 622) and Simpson (1931, p. 373), regarding *Palaeanodon* and *Metacheiromys*, respectively, observed that the long-ridged palate is *Manis*-like. Simpson (p. 325) also noted the raised alveolar border and the broad shallow groove at the edge of the palate of *Metacheiromys* and suggested that this groove may have lodged a horny plate. *Manis*, however, has a similar raised border and shallow groove but no horny plate.

If the metacheiromyids are viewed as manid ancestors, they are not "prematurely specialized" in the reduction of cheek teeth, and, on the basis of inferences from embryological evidence, neither are they "aberrantly specialized" in the large cutting canines.

"2. The proportions of the skull [of *Metacheiromys*] show none of the varied specializations of the later edentates, save for the resemblance to *Dasypus* in the broad, low occipital region. This resemblance is probably convergent. The proportions show aberrant specializations in the elongation of the post-glenoid region, which is greater than in any edentate" (Simpson, 1931, p. 368).

This statement certainly does not argue for a

palaeanodont-xenarthran relationship. Even the broad, low occipital region is due more to an artifact of preservation than to convergence. Although not shown in Simpson's figure (1931, p. 323, fig. 6), the occipital region of *Metacheiromys dasypus* is broken transversely and the bones compressed and overlapping. The cranium of *M. tatusia* is almost as high as wide. *Metacheiromys dasypus* has a single, low sagittal crest but *M. tatusia* has a smoothly rounded cranium with no sagittal crest, the condition seen in *Patriomanis* and *Manis*.

Simpson's remarks (1931, p. 321) on the general aspects of the skull of *Metacheiromys* are as follows: "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 is 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 post-glenoid part of the skull is nevertheless about half again as wide as long." These remarks could have applied equally well to *Manis* with the exception of one detail: the post-glenoid part of the skull of *Manis* is as long as wide—relatively even more elongate than in *Metacheiromys*. Simpson considered this to be an "aberrant specialization" in *Metacheiromys* because it was greater than in any living edentate. But if *Metacheiromys* is considered as an ancestor of the manids, it no longer seems aberrant in this respect.

"3. The cranial foramina [of *Metacheiromys*] 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 xenarthran in this respect" (Simpson, 1931, p. 368).

Of *Palaeanodon*, Matthew (1918, p. 625) wrote that, "the basicranial region is very near the primitive type seen in creodonts and insectivores, and it would be difficult to say whether the genus is closer to the armadillos or the pangolins." The similarity of *Metacheiromys* to *Dasypus* in this respect is clearly due to convergence. The positions of the basicranial foramina are associated with the development in *Metacheiromys* of complex bullae similar to those of *Dasypus*. Since even Simpson would have agreed that any relationship between metacheiromyids and xenarthrans would have to be through a common ancestor, the development of complex bullae in *Metacheiromys*, and the concomitant positioning of foramina, is clearly an independent derivation from that of *Dasypus*, and does not necessarily indicate relationship.

The relationships of the cranial foramina of both genera of metacheiromyids are sufficiently primitive so that *Manis* can be easily derived from either, as suggested by Simpson in the above quotation.

"4. The character of the glenoid fossa and the retention of a small but typical post-glenoid process [in *Metacheiromys*] are more primitive than in any later edentate. The absence or small size of any other basicranial processes is edentate-like" (Simpson, 1931, p. 368).

This statement applies with the same force to pangolins as to edentates. *Manis* has essentially no glenoid fossa at all and no post-glenoid process. *Manis* is also like *Metacheiromys* in the absence or small size of basicranial processes.

The condyle of the lower jaw of the metacheiromyids is more reduced than that of the early xenarthrans. This is probably associated with the greater reduction of dentition and concomitant loss of masticatory function of the jaws, a trend toward the condition seen in *Manis*.

"5. The large, compound, flask-shaped bullae [of *Metacheiromys*] are paralleled in some later edentates, but prematurely[1] acquired in *Metacheiromys* [Simpson's footnote reads, "That is, acquired too early in *Metacheiromys* to be ancestral to the later bullate forms"]. The presence of large entotympanics is very Xenarthra-like. The great 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 basicranial inflation in other orders, such as the dipodids among rodents and viverrines or mustelines among carnivores. These specializations are already indicated, but much less developed, in *Palaeanodon*. 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" (Simpson, 1931, pp. 368–369).

The auditory bullae of *Palaeanodon*, the ancestor of *Metacheiromys*, are simple, expanded, crescentic tympanics (ectotympanics of some authors), very similar to those of *Manis*. The more complex flask-shaped bullae of *Metacheiromys*, which apparently include entotympanic as well as tympanic portions, are therefore developed independently from those of the later edentates and are convergent characters which do not necessarily indicate relationship, even though the "presence of large entotympanics is very Xenarthra-like."

The complexity of the bullae may exclude *Metacheiromys*, but not *Palaeanodon*, from the direct ancestry of the Manidae. Even though small free entotympanics were reported in *Manis tricuspis* and *M. gigantea* by van der Klaauw (1931, p. 269), the bullae of these two forms are still not as specialized as those of *Metacheiromys*.

If the palaeanodonts do indeed have a large area of mastoid exposure on the occipital portion of the skull, they would be unlike *Manis*, as well as unlike the edentates, in this respect. There is, however, another interpretation. A suture separates this area of bone from the exoccipital but there is really no evidence of a suture between it and the squamosal. My interpretation is that this area of bone in palaeanodonts is not mastoid but part of the squamosal posterior to the lambdoid crest and exposed on the occipital surface of the skull.

In *Manis*, the lambdoid crest is not well developed but there is still a low ridge of bone and areas of muscular insertion to define its position. Part of this area of insertion crosses the squamosal so that part of this bone is posterior to the crest, on the occipital surface of the skull. There is no mastoid exposure on the occipital surface in *Manis*. All of the living manids have a large epitympanic recess within the squamosal bone above and posterior to the external auditory meatus. In the African species, particularly in *Manis tricuspis* and *M. tetradactyla*, this cavity is very much inflated and expanded laterally and posteriorly within the squamosal bone (fig. 26), even more than it is in *Metacheiromys*.

While this inflation in *Metacheiromys* may be analogous to that of some edentates ("functionally, but not structurally, paralleled"), it is evidently homologous to that of *Manis*. It was probably functionally the same, and, if my interpretation of the squamosal bone of *Metacheiromys* is correct, it is structurally the same. At any rate, the inflation has the same relative position in *Manis* and the metacheiromyids.

"6. The brain of *Palaeanodon*, so far as known, is much like that of *Manis*, still more like that of some armadillos, but apparently less advanced than either" (Simpson, 1931, p. 369).

I would agree that the brain of *Palaeanodon* is much like that of *Manis*, but disagree with the

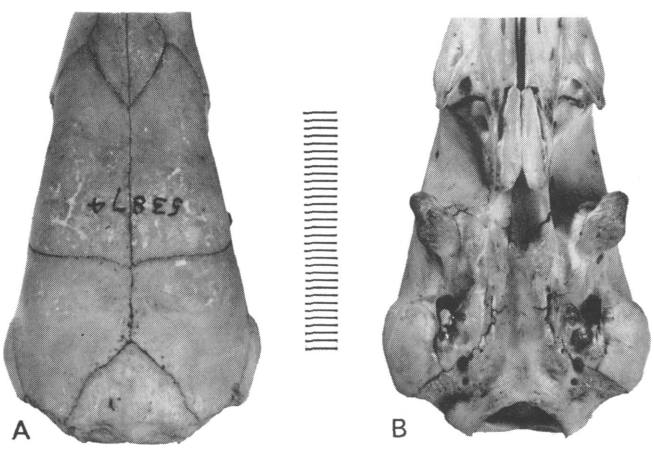

FIG. 26. *Manis tricuspis*, cranium, A.M.N.H. (M.) No. 53874. Shows inflation of epitympanic recess posteriorly and laterally within squamosal bone. A. Dorsal view. B. Ventral view. Approximately × 1; scale in mm.

statement that it is still more like that of some armadillos.

The olfactory bulbs of *Palaeanodon* appear to have been much shorter than those of armadillos. The dorsal and lateral surfaces of these bulbs were not in contact with the cribriform plate. *Manis* also has short olfactory bulbs, as did *Patriomanis*, with only the flat anterior surface contacting the cribriform plate. The olfactory bulbs of the armadillos are longer, more conical, with the cribriform plate in contact with the dorsal, lateral, and ventral surfaces.

In some of the armadillos (at least *Dasypus* and *Tolypeutes*, of which I have seen sagittally sectioned skulls), the olfactory bulbs are depressed, with sinuses between their dorsal surfaces and the upper surface of the cranium. In *Palaeanodon* and *Manis* the upper surface of the olfactory bulbs is at the same level as the upper surface of the cerebral hemispheres.

Palaeanodon has a bony tentorium projecting between the dorsal and lateral surfaces of the cerebral hemispheres and the cerebellum. This process was apparently developed to about the same degree as that of *Patriomanis*. In *Manis* the tentorium is much more strongly developed. This process is but a very low ridge in the armadillos. The cerebral hemispheres are relatively larger in *Manis* and the armadillos than in *Palaeanodon*, but *Patriomanis* is intermediate between *Palaeanodon* and *Manis* in this respect.

The nasal chamber and turbinals of *Palaeanodon* appear to have been very much like those of *Manis*.

"7. The lower jaw [of *Metacheiromys*] 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 later edentates" (Simpson, 1931, p. 369).

In reduction of dentition, of course, the lower jaws of both *Palaeanodon* and *Metacheiromys* are more Pholidota-like than Dasypoda-like. Also, as noted before, the width and strength of the condyle is less than that in the early xenarthrans, a feature probably correlated with the reduction of dentition and loss of masticatory function. In this respect, the metacheiromyids are more like the manids than like the dasypodids.

"8. The cervicals [of *Metacheiromys*] 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" (Simpson, 1931, p. 369).

That the cervicals of *Metacheiromys* are separate does not, of course, indicate relationship, even though the cervicals of the early Eocene armadillo, *Utaetus*, and those of *Manis*, are also separate. The cervicals of *Metacheiromys* are also like *Manis* in being "short, low, and wide." Simpson, in the same report (p. 330), observed that in the atlas of *Metacheiromys* the posterior foramina are superolateral to the posterior articular surfaces as in *Manis*, rather than superomedial as in armadillos. Of *Palaeanodon*, Matthew (1918, p. 627) observed that, "The spinal nerves make their exit through a notch in the posterior border of the arch, as in *Manis*, not through separate closed foramina for the upper and lower nerves, as in the modern armadillos." Simpson (1931, p. 331) described the same condition in *Metacheiromys* but did not note that it was a manid similarity. These notches are deep, extending almost half the length of the centrum, as they do in *Manis*. The articulations of the centra of the cervicals of armadillos are supplemented by separate lateral facets, even on the most posterior cervicals which are free. The palaeanodonts and manids do not have these supplementary facets. In most other details, the cervicals of the metacheiromyids are of the normal primitive placental type with no indications of the specializations seen in the xenarthrans; they are more like those of *Manis*, which more nearly retains the primitive type.

"9. The dorso-lumbar series [of *Metacheiromys*] is generally more specialized than in *Manis*, more primitive than in the Xenarthra, but with some special resemblances to the latter, even extending, in my opinion, to a foreshadowing of the xenarthrous articulations in the posterior dorsals and anterior lumbars" (Simpson, 1931, p. 369).

I find no support for the statement that the dorsals and lumbars of *Metacheiromys* are more specialized than those of *Manis*. They have no processes not also seen in *Manis*, and while the processes are more strongly developed than in the smaller species of *Manis*, they are no more strongly developed than in mature individuals of the larger species of *Manis* (e.g., *M. gigantea* and *M. temminckii*).

In his description of the anterior dorsals of

Metacheiromys Simpson (1931, p. 331) wrote that, "The postzygapophyses have a special resemblance to those of recent edentates, particularly *Manis*, and to a lesser 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." Simpson also stated that the prezygapophyseal facets are "slightly concave and face inward and upward." This is of course incorrect; they are convex and face inward and upward, the necessary condition for their articulation with the postzygapophyses of the adjacent vertebra, which he correctly described.

Not only in the anterior dorsals of *Metacheiromys*, but in all the dorsals and lumbars of both this genus and *Palaeanodon*, the nerve exits are deep notches beneath the postzygapophyses in the posterior border of the arch. Simpson's assumption that this is an edentate-like specialization toward the closed foramina of armadillos is unnecessary as well as unsupported. These notches were already as they are in *Manis*. Even if this were a specialization toward closed foramina, it would be merely convergent toward the xenarthran type.

Matthew (1918, p. 629) wrote that the zygapophyses of the lumbar vertebrae of *Palaeanodon* (A.M.N.H. No. 15137) have "large, nearly flat facets." This is incorrect; the prezygapophyses are quite strongly convex and face outward and downward. The curvature can even be seen in his figure of one of these vertebrae (1918, p. 629, fig. 44) which is reproduced here as figure 27. In *Metacheiromys*, the "prezygapophyseal facets are concave and face inward and upward, while the postzygapophyseal facets are convex and face outward and downward" (Simpson, 1931, p. 334). The lumbar zygapophyses of both metacheiromyid genera are not so strongly curved as those of *Patriomanis* and *Manis*, but are definitely developing in this direction.

In his description of *Metacheiromys*, Simpson described not a single feature of the dorsals or lumbars that is characteristically xenarthran, but relied instead on what he believed to be the "foreshadowing" of xenarthrous articulations to support his view of palaeanodont-xenarthran relationship. These are, of course, not features at all but rather an opinion of what he thought would subsequently develop. He stated (1931, p. 334) that, "While xenarthrous articulations are not definitely incipient in *Metacheiromys*, the backward projection of the anapophysis above the nerve notch and between the metapophysis and the 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." Matthew (1918, p. 629) correctly observed that in *Palaeanodon*, "There is no recognizable foreshadowing of the peculiar 'xenarthral' articulations." Because xenarthrous articulations were fully developed in *Utaetus* from the early Eocene of South America, but were not even foreshadowed in the ancestor of *Metacheiromys*, Simpson's judgment that they were incipient in *Metacheiromys* was more hopeful than anything else. Even if this interpretation could be substantiated it would be convergence toward the xenarthran type rather than a "foreshadowing" of it.

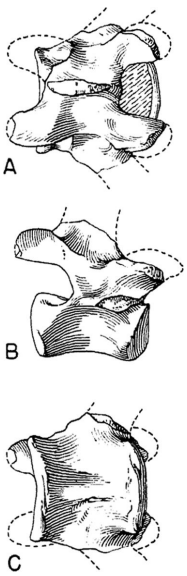

FIG. 27. *Palaeanodon ignavus*, lumbar vertebra of A.M.N.H. No. 15137. A. Dorsal view. B. Right lateral view. C. Ventral view. ×1. (From Matthew, 1918, fig. 44.)

Matthew (1918, p. 654) commented that, "The presacral vertebrae of *Manis* agree fairly well with those of *Palaeanodon* except that the

lumbar zygapophyses are strongly convex, presumably a specialization." I find no reason why *Metacheiromys* could not take the place of *Palaeanodon* in this statement.

"10. The sacrum [of *Metacheiromys*], 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 harmoniously foreshadowing all the peculiarities of the xenarthran sacrum" (Simpson, 1931, p. 369).

Again, I find no features in the sacrum of *Metacheiromys* that would make it more specialized than that of *Manis*. In the type skeleton of *Metacheiromys tatusia* there are but three sacrals, but, on the basis of a Yale Peabody Museum specimen referred to *M. marshi*, Simpson concluded that four sacrals were definitive for the genus. *Palaeanodon*, at least *P. ignavus*, has four sacrals. It is not imperative that there be one definitive number of sacrals for the genus *Metacheiromys*. *Manis* may have three or four sacrals depending on two factors: the species and the age of the individual. In the metacheiromyids, the first two sacrals are in sutural contact with the ilium and the transverse processes of the third are expanded and projecting posteriorly nearly to the pelvis but not in contact with it. In *Manis* the first three sacrals are sutured to the pelvis, two to the ilium, and one to the ischium. The transverse processes of the fourth sacral (or first caudal, depending on the individual) of *Manis* are strongly connected to the ischium by ligaments. Such was probably also the case in the metacheiromyids, as was suggested by Matthew (1918).

In the armadillos, the number of sacral vertebrae varies with the genus and species, but there are always more than the three or four of the metacheiromyids, and in the armadillos the ischium is strongly fused to the sacrum. Simpson, in his description of *Metacheiromys*, does not point out the ways in which he thought the sacrum was "harmoniously foreshadowing all the peculiarities of the xenarthran sacrum." I have failed to find them. In my opinion the sacrum of the metacheiromyids is much closer to that of the manids.

"11. The tail [of *Metacheiromys*] is of a more primitive type, with a general resemblance to the more primitive armadillos" (Simpson, 1931, p. 369).

The tail also has a general resemblance to that of *Manis*, and a more specific resemblance to this genus in the development of the broad, flat transverse processes. The tail of *Metacheiromys* is longer than the rest of the vertebral column. In no armadillo is the tail so long. Matthew (1918, p. 630) commented that in *Palaeanodon*, "The tail was evidently long and heavy, comparing more nearly with *Manis* in relative size." The median caudals of *Palaeanodon* (A.M.N.H. No. 15137), except for being smaller, are virtually identical to those of *Patriomanis*, even to the haemal sulci on the ventral surface.

"12. The scapula [of *Metacheiromys*] 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 primitive xenarthran characters. The bifid acromion parallels some Xenarthra, but may have been independently acquired" (Simpson, 1931, p. 369).

The "incipient second spine and coracoscapular notch," for the same reasons as the "incipient xenarthrous articulations" of the vertebrae, would be a convergent feature, if this is indeed the correct interpretation. I do not believe that this is an incipient second spine; the crest along the posterior border is no more accentuated than in many other mammals and, in xenarthrans, the second spine is not at the posterior edge of the scapula, but has a part of the blade posterior to it.

In *Manis* the acromion is but a short, pointed process, not even reaching the level of the glenoid. It has evidently been reduced from the type seen in the metacheiromyids, just as that of some xenarthrans has been reduced from the dasypodid type. The blade of the scapula of the Myrmecophagidae is shaped much like that of *Manis*, but the former has a second spine and the acromion is less reduced.

"13. The humerus [of *Metacheiromys*] 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 gravigrades. 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" (Simpson, 1931, pp. 369–370).

The humerus of *Metacheiromys*, considered by

Simpson to be strongly indicative of xenarthran relationships, in my opinion offers strong evidence against his view. The humeri of both *Palaeanodon* and *Metacheiromys* already have all of the positive features of the humerus of *Manis*. Simpson (1931) and Matthew (1918) both noted manid-like features in the humeri of *Metacheiromys* and *Palaeanodon*, respectively, but in his conclusions, Simpson apparently did not consider these similarities. Simpson (1931, p. 342) listed several features in which the humerus of *Metacheiromys* differs from that of *Dasypus*: "more pronounced 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." In all of these features, *Metacheiromys* is much like *Manis*, as well as *Necromanis*, *Teutomanis*, and *Patriomanis*.

In the four manid genera listed above, as well as in the metacheiromyids, the pectoral crest is elongated distally to just above the upper end of the entepicondylar bridge, and strongly turned over medially (see fig. 28, and also compare figs. 3A and 15). The lower end of this crest is limited by a definite groove or trough through which extended the tendon of the biceps muscle. If the biceps of *Metacheiromys* inserted into the radius, it would have been sharply inflected around the overhanging distal end of the pectoral crest and beneath the pectoralis major muscle, and would have tended to pull the radius medially rather than flexing it upward (fig. 28C). It seems probable that the biceps of *Metacheiromys* was inserted only into the ulna, as it is in *Manis*. Simpson (1931, p. 342) observed that, "The deltoid process [of *Metacheiromys*] as a whole is directed more toward the entepicondyle as in *Manis*, rather than toward the ectepicondyle as in most Xenarthra," but in his conclusions regarding relationships he neglected to mention this feature and its importance in relation to the musculature. In the armadillos, the delto-pectoral crest extends less than halfway down the humerus and is strongly produced laterally, extending well beyond the lateral side of the shaft (fig. 28A). The biceps muscle is not restricted from its normal insertion into the radius, although it also has a small slip inserting into the ulna. Simpson (1931, p. 340) pointed out that the bicipital groove of *Metacheiromys dasypus* is very deep and narrow, although not closed over as in armadillos. In *M. tatusia* and *M. marshi*, as well as in *Palaeanodon*, this groove is much more open though still not as broad as that of *Manis*.

The humerus of *Palaeanodon* figured by Matthew (1918, p. 644, fig. 61) shows the bicipital groove, between the greater and lesser tubercles, aligned with the flat anterior surface of the delto-pectoral crest, lateral to the distally elongated pectoral crest. What is not shown in his figure is that about 1 cm. of the shaft is restored and the head is rotated about 80 degrees to the distal portion of the humerus. The bicipital groove should be aligned so that it is medial to the pectoral crest as it is in *Metacheiromys*. A complete humerus of *P. woodi* is illustrated here as figure 28B to show the correct morphology.

The humerus of *Metacheiromys* differs from that of *Manis* in the extreme development of the supinator crest. *Palaeanodon* is more like *Manis* in this respect.

The humerus of the metacheiromyids is similar to that of armadillos only in being short and heavy, with strong muscular crests. Here the similarity ends. All of the specializations are definitely unlike those of armadillos but instead like those of the pangolins.

Matthew and Simpson both noted that the muscular crests were more strongly developed than in *Manis*. But the skeleton of *Manis*, parts of which were figured by Matthew (1918) and obviously the skeleton that he used for comparative purposes, is an immature individual. The muscular crests in a mature individual are much more strongly developed. In *Manis gigantea* the muscular crests of the humerus are as strongly develped as in *Metacheiromys*, with the exception of the supinator crest, and even here there is a small, proximally directed projection similar to, but smaller than, that of *Metacheiromys*.

"14. The radius and ulna [of *Metacheiromys*] 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" (Simpson, 1931, p. 370).

Matthew (1918, p. 631) stated that in the ulna of *Palaeanodon*, "The cuneiform articulation is much smaller than in the modern form

[*Dasypus*] and strongly oblique, facing more internad than distad." *Metacheiromys* is very similar to *Palaeanodon* in this respect, and both are similar to *Manis*. Simpson noted this manid similarity in the quotation above—the phrase in parentheses is his.

Matthew (1918, p. 632) also pointed out features in which the radius of *Palaeanodon* differs

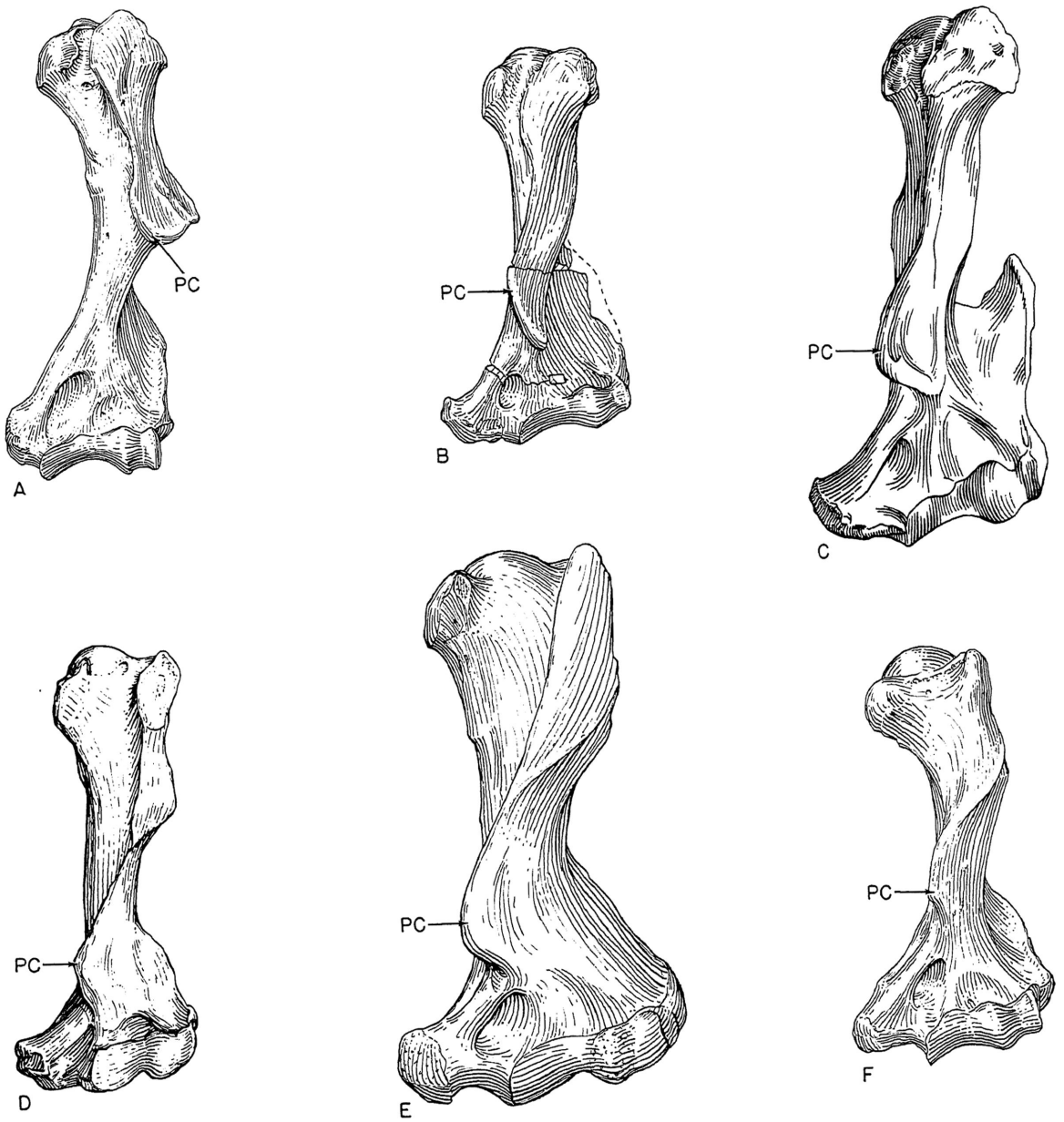

FIG. 28. Comparative anterior views of humeri. PC, pectoral crest. A. *Dasypus novemcinctus*, A.M.N.H. (M.) No. 201661. ×1. B. *Palaeanodon woodi*, humerus of type, A.C. No. 2766. ×1.25. C. *Metacheiromys dasypus*, right humerus (reversed here for easier comparison) of type, A.M.N.H. No. 11718. ×1. (From Simpson, 1931, fig. 16A.) D. *Necromanis quercyi*, type, right humerus (reversed here for easier comparison). ×1. (After Filhol, 1894, fig. 1.) E. *Teutomanis franconica*, left humerus of type. ×1. (After Quenstedt, 1885, pl. 2.) F. *Manis aurita*, A.M.N.H. (M.) No. 115628. ×1. Compare also figures 3A, 4, 15, and 16.

from that of *Dasypus*: the contraction in width of the shaft distally, the distal extremity more enlarged, the characteristic anterior crest more prominent and continuous than in modern armadillos, the distal facets for the scaphoid and lunar much larger, facing more distally and distinct from each other. In all of these features, *Palaeanodon* is very similar to *Metacheiromys* and *Manis*, except that in the latter two genera, the facets for the scaphoid and lunar are not separate, but are seen as one large, confluent, concave oval surface. Simpson (1931, p. 343) pointed out that the characters of the distal end of the radius of *Metacheiromys* were similar to *Manis*, but suggested that this was due to convergence, because the scaphoid and lunar are separate in *Metacheiromys* and fused in *Manis*. The fact that the distal articulation of the radius of *Metacheiromys* is one large oval facet indicates to me that there was very little independent movement of the scaphoid and lunar, a condition in which fusion would be more likely than if there were more independent movement of these two carpals. *Metacheiromys* is intermediate between *Palaeanodon* and *Manis*; the two carpals probably functioned as they do in *Manis*, but were separate as they are in *Palaeanodon*.

In the radius of *Patriomanis*, as well as in the radius (cf. *Teutomanis*) described by Helbing (1938), the proximal end is more transversely expanded than in *Manis*. These two fossil genera are much like *Metacheiromys* in this respect.

"15. The carpus [of *Metacheiromys*] 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 primitive Xenarthra" (Simpson, 1931, p. 370).

Simpson remarked in his description (p. 345), but did not repeat in his conclusions, that the lunar of *Metacheiromys*, although not fused to the scaphoid, is more like the lunar of *Manis*. And as mentioned before, although these two carpals were not fused, they must have had very little independent movement and functioned much as they do in of *Manis*.

Because the distal articulation of the ulna of *Palaeanodon* and *Metacheiromys* is similar to *Manis*, as pointed out by Matthew and Simpson, respectively, then the cuneiform that articulates with it should also be similar to that of *Manis*. Such is the case. Matthew (1918, p. 632) pointed out that the cuneiform of *Palaeanodon* is "very much like that of *Manis*."

The other carpals of the metacheiromyids have no specializations that are either particularly armadilloid or *Manis*-like.

"16. Despite Winge, the proportions of the digits [of *Metacheiromys*], 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, *Metacheiromys* is aberrant, but *Palaeanodon* is more primitive in this, and probably in all parts of the feet. The tendency toward ulnar rotation of the manus is distinctly Xenarthra-like" (Simpson, 1931, p. 370).

Admittedly, the feet of *Metacheiromys* are "more like the primitive Xenarthra than like *Manis*," but this is not a very meaningful comparison. The primitive Xenarthra more nearly retain the primitive condition seen in *Metacheiromys*, but so do the primitive manids. The specialization of the metapodial-phalangeal articulations of *Manis* are evidently a late Tertiary development. The metapodial-phalangeal articulations of *Myrmecophaga* are much like those of *Manis*. If the metacheiromyid-manid relationship is denied because *Manis* has more specialized feet, then, by the same token, the relationship of *Myrmecophaga* to the dasypodids might be denied.

It will be recalled that the armadillo-like metapodials of *Teutomanis* were referred by Ameghino (1905) to a new genus, "*Galliaetatus*," which he considered to be an armadillo. Ameghino held that it was impossible for an animal with the humerus of a manid to have metapodials so much like those of the armadillos. This same argument, applied to the myrmecophagans, would deny their relationship to the armadillos. But the humerus of *Teutomanis* has been found at other localities in Europe associated with armadillo-like metapodials (more correctly, metapodials lacking the specializations seen in *Manis*). The North American

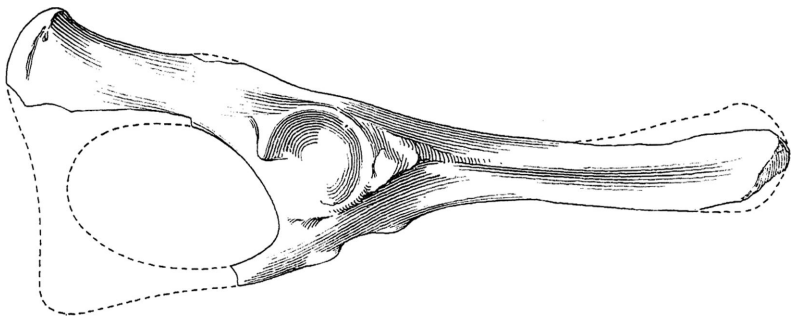

FIG. 29. *Palaeanodon ignavus*, A.M.N.H. No. 15088, right side of pelvis. Right lateral view. ×1. (From Matthew, 1918, fig. 49.) Compare with figure 21B.

manid, *Patriomanis*, also lacked the specializations of the metapodial-phalangeal articulations seen in *Manis*. These two fossil manids had metapodials more similar to those of *Metacheiromys* than to those of *Manis*.

The compressed claws of the forefeet of *Metacheiromys* are also similar to those of *Manis*, except that in the former the claws are not fissured and in the latter they are deeply fissured. The only preserved claw of *Patriomanis* is broken but could have had only a very shallow fissure, if any.[1] As Simpson noted, the claws of *Metacheiromys* are not like those of armadillos but more like those of the ground sloths. The ground sloths are, then, convergent in this respect.

The tendency toward ulnar rotation in *Metacheiromys* is distinctly Pholidota-like as well as "distinctly Xenarthra-like." In fact, the living pangolins, which always walk on the outside (ulnar side) of the front feet, show even more ulnar rotation than do the armadillos.

"17. The pelvis [of *Metacheiromys*] 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" (Simpson, 1931, p. 370).

In a mature individual of *Manis*, particularly *M. temmenckii* or *M. gigantea*, both the ischia and ilia are strongly everted and crested—as much, in fact, as in the armadillos. If manid characters are not restricted to those seen in an immature individual, then *Metacheiromys* also has many manid characters.

In *Metacheiromys* the ischium is relatively shorter (with respect to the ilium) than in *Palaeanodon*; in *Manis* it is even shorter. In *Metacheiromys*, the shaft of the pubis descends from beneath the ventral part of the acetabulum; the same relationship is seen in *Patriomanis*. In *Manis* the pubis is more posterior; in the armadillos, more anterior. In a specimen from the middle Miocene of Mont-Ceindre, France, allocated by Ameghino to "*Galliaetatus*" (= *Teutomanis*), the pubis has the same relationship as that of *Patriomanis* and *Metacheiromys*. This specimen also has a dorsal crest on the ischium.

The fragment of pelvis of *Patriomanis* is remarkably similar to the same part of the pelvis of *Palaeanodon* (compare figs. 29 and 21B).

The pubic symphysis of *Manis* is short, like that of *Patriomanis*, the metacheiromyids, and the armadillos.

"The fusion of one or two more caudals" would still leave *Metacheiromys* with fewer sacrals than any known xenarthran, but this genus needs no more fused caudals to be like *Manis*.

The "incipient caudo-ischial union" of *Metacheiromys* is really not a character but a speculation concerning future development. If it were to develop, it would be convergent to the xenarthran type, which was already developed. The transverse processes of the fourth sacral vertebra of *Metacheiromys* have the same relationship to the ischia that they have in *Manis*; the bones are not in contact but were probably connected by ligaments in *Metacheiromys* as they

[1]The two additional distal phalanges of *Patriomanis*, collected in 1969 as noted in footnotes on pages 466 and 481, are both quite deeply fissured.

are in *Manis*. The armadillos have at least three, and some as many as five, sacral vertebrae completely fused to the ischium.

The pelvis of *Metacheiromys* is not unlike that of *Manis*, if the *Manis* used for comparisons is a mature individual. The fossil manids, *Patriomanis* and *Teutomanis*, were apparently even more like *Metacheiromys*. If the metacheiromyid pelvis is viewed as that of an ancestral manid, it is not necessary to postulate the "fusion of one or two more caudals" and the "incipient caudo-ischial union." *Metacheiromys* and *Palaeanodon* were already like *Manis* in these features.

"18. The femur [of *Metacheiromys*] is very unlike that of *Manis*, suggestive of the armadillos but much less specialized, very close to that of Miocene gravigrades but slightly more primitive in the less marked anteroposterior compression" (Simpson, 1931, p. 370).

The metacheiromyid femur is indeed unlike that of *Manis* in a number of features, but here again intermediate stages are known.

The third trochanter of *Palaeanodon* is a strong process quite high on the shaft; in *Metacheiromys* it is relatively smaller and lower on the shaft; in a femur referred to *Necromanis* from the Phosphorites of Quercy, France, the third trochanter is even more reduced and more distally placed; in the femur of *Teutomanis*, the third trochanter is small and quite distally placed on the shaft (fig. 30). In *Manis* the femoral insertion of the gluteus maximus muscle (which inserts into the third trochanter in animals having this process) is into a swelling on the lateral surface of the shaft just above the lateral condyle (Humphry, 1870; Windle and Parsons, 1899).

The second (lesser) trochanter is also progressively reduced in size from *Palaeanodon*, where it is a relatively large flat process, to *Manis*, where it is a small conical process.

The greater trochanter of *Palaeanodon* extends above the head of the femur; in *Metacheiromys* it is level with the head; in *Manis* it is lower than the head. The head is broken from the femur of *Necromanis* so this relationship cannot be determined, and the femur of *Teutomanis* is lacking the upper extremity.

Manis lacks the digital fossa, which is present in the metacheiromyids. The femur of *Teutomanis* still had a digital fossa.

The shaft of the femur of the metacheiromyids is anteroposteriorly compressed to about the same degree as that of the manids. Simpson (1931, p. 352) wrote that, "The shaft of the femur [of *Metacheiromys*] is flattened anteroposteriorly, rather more than in *Dasypus* or *Tatu*, less than in gravigrades or *Manis*." I cannot reconcile this statement with my observations; the femur of *Manis* and the metacheiromyids is less flattened than that of any of the armadillos with which I have compared them.

In his description of the femur of *Metacheiromys*, Simpson (1931, pp. 352–353) observed that, "As in *Manis*, the popliteal surface is plane" and "The distal end of the femur is almost exactly like that of *Dasypus* and also very similar to *Manis*, save for the narrower patellar groove." He also pointed out that the patellar trochlea of *Metacheiromys* is directed toward the head, as in *Manis*, rather than toward the greater trochanter as in armadillos. *Palaeanodon* is like *Metacheiromys* and the manids in this respect. In Simpson's description, the femur of *Metacheiromys* is more like that of *Manis* than it is in his conclusion quoted above.

The femur of *Myrmecophaga* is much like that of *Manis*; in both genera there is no digital fossa, no third trochanter, the greater trochanter is lower than the head, and the second trochanter is relatively small. The development of the femur of *Myrmecophaga* from the dasypodid type was paralleled by that of *Manis* from the metacheiromyid type.

Figure 30 shows the femora of several taxa so that the positions and sizes of trochanters, direction of patellar trochlea and other features can be compared.

"19. The crus [of *Metacheiromys*] differs from that of the armadillos only in being slightly more primitive. Thus, the tibia and fibula are unfused or only partly united. The antero-superior tubercle is less expanded, the proximal part of the tibia is somewhat less produced anteroposteriorly, the distal end of the tibia less transverse, etc." (Simpson, 1931, p. 370).

That the crus of *Metacheiromys* is more primitive than that of armadillos (i.e., lacks armadilloid specializations) does not necessarily imply that it is ancestral. The tibia and fibula of *Manis* are separate as they are in the metacheiromyids.[1]

[1]Matthew (1918, p. 635) reported that the fibula of *Palaeanodon* is fused to the tibia at the distal end. However, in several other specimens in the American Museum collections, and also in *Palaeanodon woodi* Guthrie, 1967, the tibia and fibula are unfused. In no specimen of *Metacheiromys* are the tibia and fibula fused at either end.

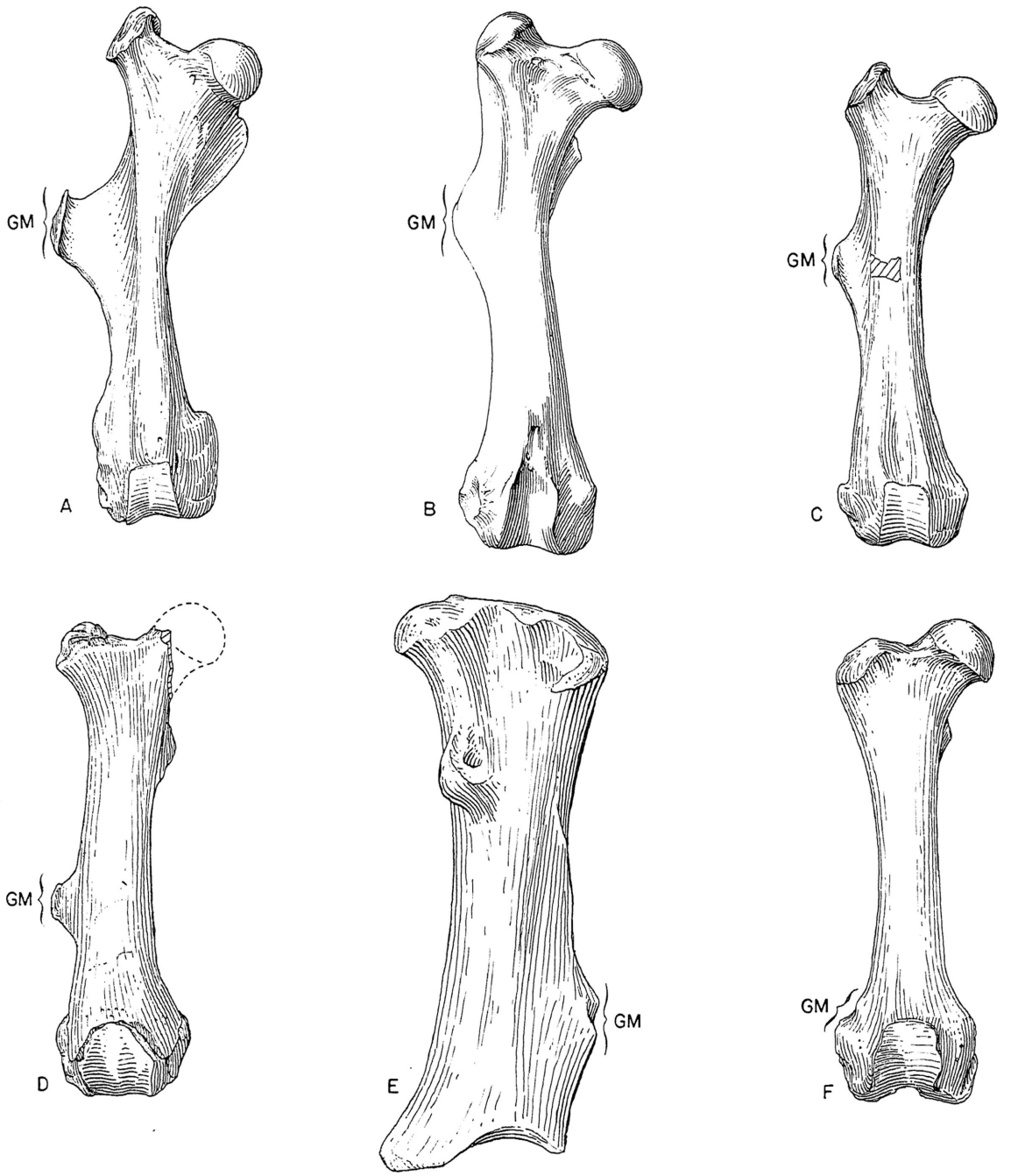

FIG. 30. Comparative views of femora. GM, area of insertion of gluteus maximus muscle. A. *Dasypus novemcinctus*, A.M.N.H. (M.) No. 201661, right femur. Anterior view. × 1. B. *Palaeanodon ignavus*, A.M.N.H. No. 15088, right femur. Anterior view. × 1. (From Matthew, 1918, fig. 65B.) C. *Metacheiromys tatusia*, A.M.N.H. No. 11719, left femur (reversed here for easier comparison). Anterior view. × 1.5. D. *Necromanis*, right femur. Anterior view. × 1. (After Filhol, 1894, fig. 14, and Ameghino, 1905, fig. 46.) E. *Teutomanis*, right femur. Posterior view. × 1. (After Schlosser, 1904, pl. 26, fig. 11.) F. *Manis aurita*, A.M.N.H. (M.) No. 115628, right femur. Anterior view. × 1.

The other features of *Metacheiromys* that Simpson listed as being more primitive than in armadillos, are like those of *Manis*.

Manis and apparently also *Patriomanis* have an ossicle in the tendon of the popliteus muscle that articulates with the tibia on the posterior surface at the proximal end. This was discussed in the description of *Patriomanis*, and the articular facet can be seen in figure 22B. Both *Metacheiromys* and *Palaeanodon* apparently also had this "sesamoid." In all of the tibii of both these genera that I have been able to study (A.M.N.H. Nos. 11549, 14713, 15088, 15137, 16832, and A.C. No. 2766), there is a downward extension of the lateral condylar surface very much as in *Manis* and *Patriomanis*. This is especially apparent in a tibia of *Palaeanodon ignavus* (A.M.N.H. No. 14713), in which this "sesamoid" facet is separate from the lateral condylar surface.

The shaft of the tibia of the metacheiromyids is more laterally compressed than in *Manis*, but very similar to that of *Patriomanis*. In the metacheiromyid tibia, a sharp crest extends upward from the distal fibular facet and merges with the lateral side of the shaft. This is also seen in *Patriomanis* (figs. 23B, C.)

The distal articular surface of the fibula of both *Palaeanodon* and *Metacheiromys* faces inward, as in *Manis*, rather than distally as it does in armadillos. Posteromedially at the distal end of the tibia of *Manis* and the metacheiromyids there is a single deep malleolar sulcus, whereas in the armadillos and, as far as I can determine, in all the xenarthrans there are two deep, parallel sulci here.

Simpson (1931, p. 355) described the fibula of *Metacheiromys* as a "slender, straight rod, much like that of *Manis*, less curved and crested than in most xenarthrans" and noted that, "The lateral malleolus has a distinct process projecting straight laterally, as in *Manis* but stronger." In the larger living manids, however, the lateral malleolus is as strong as in the metacheiromyids.

The crus of the metacheiromyids is certainly more like that of the manids than like that of the armadillos. The tibia of *Patriomanis* is perhaps even more like the metacheiromyid tibia than like the tibia of the living manids.

"20. The astragalus of *Palaeanodon* is approximately intermediate between a generalized insectivore type and that of the armadillos. In *Metacheiromys* the astragalus is still more definitely armadilloid, although more 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" (Simpson, 1931, p. 371).

In my opinion, the astragali of *Palaeanodon* and *Metacheiromys* are so similar that I would hesitate to say which was more armadilloid. If, as Simpson thought, the astragalus of *Metacheiromys* is more armadilloid than that of *Palaeanodon*, it would then be demonstrably convergent, since Simpson would have agreed that *Palaeanodon* is ancestral to *Metacheiromys* and that these genera could be related to the armadillos only through a common ancestor. Figure 31 compares the astragali of *Dasypus*, *Palaeanodon*, and *Manis*.

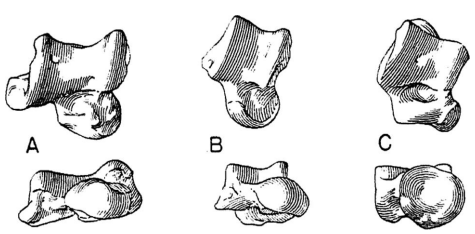

FIG. 31. Comparative anterior and distal views of right astragali. A. *Dasypus novemcinctus*, A.M.N.H. (M.) No. 20357. ×1. (From Matthew, 1918, fig. 67A.) B. *Palaeanodon ignavus*, A.M.N.H. No. 15137. ×1. (From Matthew, 1918, fig. 67B.) C. *Manis pentadactyla*, A.M.N.H. (M.) No. 31815. ×1. (From Matthew, 1918, fig. 67C.) Compare also figure 6.

The astragalus and calcaneum from the Miocene of Europe that were described by Helbing (1938), reproduced in this paper as figures 6 and 7, appear to have had both metacheiromyid and manid similarities, insofar as I can determine from the illustrations. The calcanea of *Patriomanis* and *Teutomanis* also have palaeanodont similarities (see fig. 32, and compare also figs. 7 and 25). As discussed, the metacheiromyids lacked the specializations seen in the feet of *Manis*, but so do the primitive manids, which are more like the metacheiromyids in this respect.

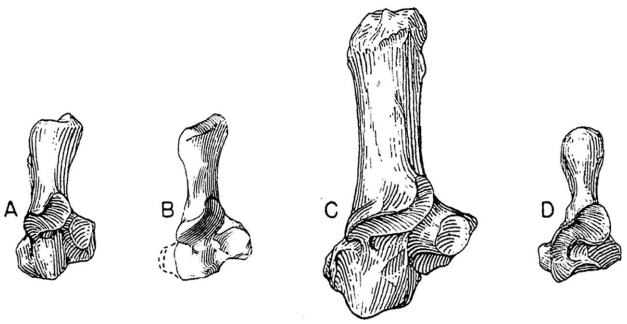

FIG. 32. Comparative anterior views of right calcanea. A. *Dasypus novemcinctus*, A.M.N.H. (M.) No. 201661. ×1. B. *Palaeanodon ignavus*, A.M.N.H. No. 15137. ×1. (From Matthew, 1918, fig. 68B, with external projection outlined from A.M.N.H. No. 16832 and other calcanea.) C. *Teutomanis*. ×1. (After Schlosser, 1904, pl. 26, fig. 13.) D. *Manis pentadactyla*, A.M.N.H. (M.) No. 184959. ×1. Compare also figures 7 and 25.

RELATIONSHIPS

PALAEANODONT-XENARTHRAN AFFINITIES

IT CANNOT BE DENIED that the metacheiromyids (especially *Metacheiromys*) have some points of resemblance to the armadillos. However, when interpreting the meaning of these similarities, we must keep in mind an important fact: The known metacheiromyids cannot be directly ancestral to the Xenarthra; they are too unevenly specialized and also appear too late in the record. None of the similar characters can therefore be attributed to an ancestor-descendant relationship between Palaeanodonta and Xenarthra. Both Matthew (1918) and Simpson (1931) realized that any relationship would have to be through a common ancestor.

The similarities between the metacheiromyids and xenarthrans are then limited to these two kinds of characters: (1) similar characters inherited from a common ancestor-homology, and (2) similar characters independently acquired in the two groups—convergence. The metacheiromyid-xenarthran similarities are due to both kinds of characters, but none of these is, in my opinion, indicative of especially close relationship.

That two groups are related by a common ancestor can be determined only if they have in common some homologous character or characters derived from the common ancestor, and these characters must be other than primitive generalized mammalian characters that would be equally suggestive of a relationship to other groups.

Even a defender of Simpson's view, after reading first his description of *Metacheiromys* and its comparisons with xenarthrans, would have to admit that in his conclusions he clearly overstated the evidence for a xenarthran-palaeanodont relationship. Almost all of Simpson's statements regarding armadilloid similarities of *Metacheiromys* (quotations 1 through 20 of the previous section of this report) are immediately qualified by phrases such as, "but more primitive," "aberrantly or prematurely specialized," "much less specialized," or "must nearly represent the ancestral condition of the most primitive xenarthrans."

Since the only possible relationship between Palaeanodonta and Xenarthra is through a common ancestor, any xenarthran similarities developed within the *Palaeanodon-Metacheiromys* phylum would be convergent. Some of the characters considered by Simpson to indicate xenarthran affinities are of this kind; he implied homology where only analogy exists.

Other similarities used by Simpson in his argument for a special relationship between palaeanodonts and xenarthrans are primitive characters that are equally suggestive of relationships to many other groups. That these common characters are primitive does not deny the relationship but neither does it support it. These characters should not be given undue emphasis.

Simpson also cited what he considered to be "incipient" xenarthran characters in *Metacheiromys*. These, aside from the question of their existence, do not, in this case, indicate relationship, as emphasized previously. They are incipient xenarthran characters only if they subsequently developed into typical xenarthran characters. As these characters were already fully developed in the Xenarthra, their incipient state in *Metacheiromys* is equivocal at best and, even if accepted, would be convergence rather than homology.

Simpson (1931, pp. 367–368) stated that the Palaeanodonta ". . . have, either typically developed or incipient, all the general ordinal characters of the Xenarthra," but a few pages later (p. 371) stated that "*Metacheiromys* is so early and primitive that the specifically xenarthran characters are indicated rather than typically defined." Not only are these two statements inconsistent, but the first is untrue and the second, misleading. The palaeonodonts have no typically defined ordinal xenarthran characters (the incipient ones have already been discussed), and the lack of these cannot be because *Metacheiromys* is "so early and primitive." Xenarthrans had these characters typically developed even earlier, and *Metacheiromys* is not more primitive but instead specialized in different ways.

The palaeanodonts and xenarthrans are similar in habitus characters, such as short, stout limb bones and reduction of dentition, but here any special similarity stops. The limbs are specialized in different ways and the reduction

of dentition follows a different pattern. Had the palaeanodonts had unreduced dentition (as the ancestors of the Xenarthra must have had), I doubt that they would ever have been seriously considered as close relatives of the Xenarthra.

Because two groups cannot have common ancestry without also having common geographic origin, the paleogeographic evidence must be considered. The palaeanodonts apparently could not have reached South America after the early Paleocene. Simpson commented (1931, p. 378) that the Xenarthra were ". . . probably derived in the late Cretaceous or early Paleocene from the Palaeanodonta, which in turn were derived from Cretaceous Insectivora." Although there is as yet no positive evidence to deny this relationship, neither is there any paleontological evidence to support it. Matthew (1918, pp. 656–657) regarded the edentates as derivatives of some unknown insectivore allied to the Leptictidae or Pantolestidae. There are no features of either the palaeonodonts or xenarthrans to indicate that they are more closely related to each other than either is to the Insectivora. A common ancestor of the palaeanodonts and xenarthrans would probably not be recognized as a palaeanodont or a xenarthran, but rather as an early Paleocene or Cretaceous insectivore.

XENARTHRAN AFFINITIES

The oldest definite remains of Xenarthra are armadilloid scutes from the late Paleocene Río Chico Formation of Patagonia. An armadillo, *Utaetus*, from the early Eocene Casa Mayor Formation of the same area, is sufficiently well known to show that it had already acquired all of the fundamental xenarthran and armadilloid characters. In the words of Simpson (1948, p. 87), "Almost all the positive features shared by all recent armadillos, and hence presumably present in their immediate common ancestry, are displayed in characteristic form in this Eocene relative: e.g., strong dermal armor of armadilloid structure and pattern, degenerate and rootless teeth, xenarthrous vertebrae, scapula with two spines and very large acromion, ischiocaudal suture, large third trochanter of femur, and highly characteristic astragalus. With only isolated scutes, it was perhaps possible, as Matthew implied, that we were dealing with primitive forms only superficially armadillo-like, but now it is obvious that *Utaetus*, at least, is a real armadillo in every respect."

Simpson (1948, p. 88) listed several features of *Utaetus* that he thought showed some special resemblance to the palaeanodonts and supported his view that the Xenarthra were derived from the Palaeanodonta. Some of these are primitive mammalian characters: presence of enamel on teeth and unfused cervicals. Others are characters in which *Utaetus* is more palaeanodont-like than are later armadillos. They do not indicate relationship but rather that both *Utaetus* and the palaeanodonts lack specializations seen in later armadillos. Simpson believed that *Utaetus* was intermediate between Recent armadillos and palaeanodonts, but "distinctly closer to modern armadillos than to any known palaeanodont" (1948, p. 88).

Even the earliest known xenarthrans had specializations that were not present in the palaeanodonts. Likewise, the palaeanodonts have specializations not seen in the Xenarthra. The only specialization common to both groups is reduction of dentition. But the pattern of reduction of dentition is different and probably an independent development in each group.

The earliest xenarthrans have no features to indicate that they were more closely allied to the Palaeanodonta than to the Insectivora. The Palaeanodonta and Xenarthra were probably independently derived from the Insectivora (that is, the closest common ancestor is probably not within the Edentata), but the group or groups of insectivores from which they were derived is not yet definitely known and, so far as I can determine, is practically unresearched.

PALAEANODONT-MANID AFFINITIES

Matthew (1918) was the first, and until now, apparently the last, at least in print, to consider the Manidae as derivatives of the Palaeanodonta. He commented (1918, pp. 653–654) that, "So far as the skull is concerned, there is nothing to prevent our regarding *Palaeanodon* as the direct ancestor of *Manis*." Insofar as I can determine, there is no feature of any part of the osteology of *Palaeanodon* that would preclude its being directly ancestral to *Manis*.

Simpson (1931, p. 372) wrote that, "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 statement is without defense. *Metacheiromys* has only two specializations that would appear to prevent its being directly ancestral to *Manis*: the more complex auditory bullae and the more extreme development of the supinator crest of the humerus. All of the other specializations of *Metacheiromys* and all of the specializations of *Palaeanodon* are also present in *Manis*. And perhaps as important, the metacheiromyids appear too late to be directly ancestral to the Xenarthra but are not excluded from the direct ancestry of the Manidae in this way.

Simpson (1931, p. 372) concluded that, "With few possible exceptions, the resemblances [of *Metacheiromys*] 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*." *Manis* does retain many primitive features, but the specializations of the palaeanodonts are decidedly more *Manis*-like than armadillo-like, as shown in a previous section of the present paper. The characters of *Metacheiromys* that Simpson considered to be unlike those of armadillos are like those of *Manis*.

Metacheiromys is intermediate between *Manis* and *Palaeanodon* in some respects: reduction of dentition, postglenoid elongation of cranium, more distally elongated pectoral crest of humerus, single concave distal articular surface of radius, reduction in height of greater trochanter of the femur, reduction and more distal position of the third trochanter of the femur, among others pointed out in previous discussions.

Matthew (1918) discussed the European Tertiary manid remains, and cited features that he believed to be intermediate between palaeanodonts and *Manis*. Simpson (1931, p. 374) rejected this evidence by replying that the European remains were unlike those of *Manis* in most features and denied that intermediate stages had been shown to exist. Since I consider Matthew's observations to be valid, I will reintroduce them and further support them by evidence from *Patriomanis*. Matthew (1918, p. 654) commented that the limb bones of *Manis* are more simple than those of palaeanodonts in the lesser development of humeral crests, femoral trochanters, cnemial crest of the tibia, and so on. He considered this to be a secondary simplification and cited the European Tertiary manids as intermediates. Since Matthew's specimen of *Manis* was a young individual, the decrease in development of crests is, in fact, not so great as he thought. *Patriomanis*, however, does support his conclusions. The femoral trochanters are discussed in an earlier part of this report. The reduction of the third trochanter of *Manis* is a specialization and its presence in the palaeanodonts, a primitive feature.

It is difficult to improve on Matthew's comments regarding the astragalus and metapodials of *Manis*. He wrote (1918, p. 654) that, "The peculiar type of astragalus in *Manis* and the prominent distal keels of the metapodials both resemble very closely the Miocene groundsloths, and differ widely from palaeanodonts and armadillos. But these peculiarities in the groundsloths are undoubtedly derived from the more primitive armadillo type; it is reasonable to conclude that in *Manis* they are also derived from the primitive armadilloid type seen in *Palaeanodon*; and here again the European Tertiary genera offer confirmatory evidence, for in *Galliaetatus* [=*Teutomanis*] the metacarpals appear to be quite armadilloid, although the limb bones of the same skeleton are far advanced toward the type of *Manis*." *Patriomanis* can now take the same position as *Teutomanis* in this argument.

The Myrmecophagidae and *Manis* are even more convergent than are *Manis* and the Miocene ground sloths. *Myrmecophaga* and *Manis* both have similar astragali, similar prominent keels on the metapodials, no third trochanter, the greater trochanter lower than the head of the femur, no digital fossa, similar shape of the blade of the scapula, and complete loss of dentition. The similarity between *Manis* and the metacheiromyids is greater than that between the myrmecophagids and the dasypodids.

By early Oligocene the manids were apparently already much like *Manis* in all specializations except those of the feet. The vertebral articulations were of the "embracing" type. The muscular crests of the limb bones were similar to those of *Manis* but slightly more strongly developed. The skull was apparently much like that of *Manis*.

In the metacheiromyids the feet are primitive as in the earliest manids, but the limbs already have most of the manid specializations. The dentition of *Metacheiromys* was reduced to

canines and a few very small pegs, and the zygapophyses of the vertebrae were curved but not yet of the "embracing" type. In kinds and pattern of development of specializations, the metacheiromyids have what would be expected in an ancestor of the Manidae.

The presence of a pangolin in North America does not, of course, in itself prove the palaeanodont-manid relationship, but does improve the paleogeographic evidence and makes the relationship far more credible. This occurrence does no damage to traditional views on continental connections and migrations. The early Oligocene was a period of extensive dispersal of mammals between the Holarctic land masses (Simpson, 1947). This time coincides with the presence of a pangolin in North America and the first record of the group in Eurasia.

Pocock (1924) concluded, on the basis of external characters, that the living Asiatic pangolins were more primitive than those of Africa and that Asia rather than Africa was the original home of the order Pholidota. Now that the ancestors of the Manidae, as well as one of the oldest known manids, are known in North America, the most parsimonious conclusion would be that this continent was the place of origin of the order Pholidota and also of the family Manidae. To assert this without flexibility, however, would be to give negative evidence the force of fact. Too little is yet known about the late Paleocene and early Eocene of Asia. Since the ancestor of the palaeanodonts is yet unknown, we must still entertain the possibility that Asia was the original home of the order and that *Palaeanodon* was a late Paleocene or early Eocene migrant to North America. It is also possible that an unknown Asiatic palaeanodont gave rise to the manids which then dispersed to Europe and North America in the early Oligocene. These possibilities, although real, are founded only on negative evidence. The only conclusion with positive evidence (not proof) is that the order Pholidota originated in North America with the development of the palaeanodonts which later gave rise to the Manidae.

The apparent close relationship between *Patriomanis* and the European fossil forms gives support to the idea that the dispersal of the manids, either to North America or from North America, was in the early Oligocene rather than early Eocene, the next older major period of intercontinental dispersal. If the environmental requirements of early Oligocene pangolins were similar to those of the living pangolins, then the route of dispersal, whether it be the Bering corridor or the currently much-discussed North Atlantic connection, must have had a climate different from that of today.

If considered as xenarthran relatives, the palaeanodonts have many aberrant features and premature specializations, as noted by Simpson (1931, pp. 368–371). If the palaeanodonts are considered as manid ancestors, these features are no longer aberrant and the specializations are no longer premature. There is nothing to prevent our considering the palaeanodonts as direct ancestors of the manids. Temporal and paleogeographic considerations are not violated, and at the same time there is, in my opinion, a great deal of morphologic evidence to support the relationship.

PHYLOGENY AND TAXONOMY

IN LINNAEAN TIMES, *Manis* was closely associated with the South American anteaters, but its distinctive characters led to separation at progressively higher taxonomic levels until Pholidota was made a distinct order by Weber in 1904. Matthew (1918) still considered the Pholidota and Xenarthra to be related, with the Palaeanodonta directly ancestral to the manids and linked by common ancestry to the Xenarthra. Simpson (1931) considered the Palaeanodonta and Xenarthra to be related through a common ancestor but that the manids were probably not related at all to the palaeanodonts. My views on relationships differ from those of Simpson and are only partly in accord with those of Matthew.

The manids can be derived directly from *Palaeanodon*, and *Metacheiromys* is even more like *Manis* in all features except the auditory bullae and enlarged supinator crest of the humerus. Not only are there no features preventing this derivation but, as previously discussed, there are many features to support it.

That the metacheiromyids and xenarthrans are related through a common ancestor within the Edentata cannot be absolutely denied but neither is there evidence in its favor. The closest common ancestor would probably be within the Insectivora.

It seems more rational to classify the palaeanodonts under the Pholidota on the basis of positive morphologic evidence rather than under the Edentata where it is necessary to rely on a hypothetical common ancestor that cannot be positively disproved. Transferral of the palaeanodonts to the Pholidota brings into this order not only the Metacheiromyidae but another family, the Epoicotheriidae, which is briefly discussed in the present paper.

METACHEIROMYIDAE WORTMAN, 1903

The Metacheiromyidae includes only two genera, *Metacheiromys* and *Palaeanodon.*

EPOICOTHERIIDAE SIMPSON, 1927

The first genus of the family to be described, *Epoicotherium* Simpson, 1927, was originally called *Xenotherium* by Douglass in 1905, but the name was preoccupied (Ameghino, 1904). The type species, from the early Oligocene (Chadronian) of Montana, was described as a monotreme by Douglass (1905), later referred to the Chrysochloridae (Matthew, 1906; Gregory, 1910) and finally identified as an edentate related to the Metacheiromyidae (Zdansky, 1926; Simpson, 1927; Matthew, 1928). The genus is also now known from an undescribed partial skeleton from the early Oligocene (Chadronian) of Wyoming in the American Museum of Natural History. This specimen is similar in some skeletal features to *Pentapassalus* (discussed below), which in turn has many points of resemblance to the metacheiromyids.

Xenocranium Colbert, 1942, from the middle Oligocene (Orellan) of Wyoming, is apparently quite closely related to *Epoicotherium* and is similar in some respects but more specialized in the auditory region.

Pentapassalus Gazin, 1952, from the early Eocene (Wasatchian) of Wyoming, is similar to the metacheiromyids in many features but is like *Epoicotherium* in the more triangular skull and elongated entepicondyle of the humerus. The undescribed skeleton of *Epoicotherium* supports Gazin's conclusion that *Pentapassalus* belongs in the Epoicotheriidae.

Tetrapassalus Simpson, 1959, from the middle Eocene (Bridgerian) of Wyoming, is incompletely known but was probably related to *Pentapassalus.*

Tubulodon Jepsen, 1932, from the early Eocene (Wasatchian) of Wyoming, was originally considered to be a tubulidentate because of tubular structures in the teeth. Gazin (1952, p. 44) commented that *Pentapassalus* has similar structures in the teeth, but concluded that they were probably of postmortem development and, at any rate, not homologous to those of the aardvarks. *Tubulodon* is not definitely an epoicotheriid but this is a reasonable possibility, in accord with morphologic and paleogeographic evidence, and seems to be the best suggestion that can now be advanced.

MANIDAE GRAY, 1821

The living and fossil genera of the family Manidae have been discussed in a previous section of the present report.

CLASSIFICATION OF THE ORDER PHOLIDOTA

To balance the classification it is necessary to either discontinue the use of the term Palaeanodonta as a suborder that includes the Metacheiromyidae and Epoicotheriidae or to propose a new suborder to include the Manidae. Since the mutual affinities of the three families are not yet clearly known, I have chosen the former alternative for the present. The Manidae are quite clearly derived from the Metacheiromyidae but whether this relationship is closer than that between the Metacheiromyidae and Epoicotheriidae remains to be determined. The Manidae are more specialized and differ more morphologically from the other two families than the other two families do from each other but this morphological difference is probably not directly proportional to the closeness of relationship. The Manidae were almost certainly derived from the Metacheiromyidae after the Metacheiromyidae and Epoicotheriidae were already distinct from one another. When the Epoicotheriidae are reviewed, the mutual relationships of the three families should be better understood.

The following classification includes all of the genera that can be confidently considered to belong to the order Pholidota and the approximate known time ranges of these genera. Additional information and references on the higher categories can be found in Simpson's classification (1945). This classification, with three families not further grouped, should not imply that the relationship between the families is equal but rather that grouping into suborders would imply relationships that are not yet well supported.

Order PHOLIDOTA Weber, 1904, p. 412.
- Family Metacheiromyidae Wortman, 1903, p. 347.
  - *Palaeanodon* Matthew, 1918. Late Paleocene-early Eocene, North America.
  - *Metacheiromys* Wortman, 1903. Medial Eocene, North America.
- Family Epoicotheriidae Simpson, 1927, p. 285.
  - *Pentapassalus* Gazin, 1952. Early Eocene, North America.
  - *Tetrapassalus* Simpson, 1959. Medial Eocene, North America.
  - *Epoicotherium* Simpson, 1927 (=*Xenotherium* Douglass, 1905, *nec* Ameghino, 1904). Early Oligocene, North America.
  - *Xenocranium* Colbert, 1942. Medial Oligocene, North America.
- Family Manidae Gray, 1821, p. 305.
  - *Patriomanis* Emry, this report. Early Oligocene, North America.
  - *Necromanis* Filhol, 1894. ?Early Oligocene, Europe.
  - *Leptomanis* Filhol, 1894. ?Early Oligocene, Europe.
  - *Teutomanis* Ameghino, 1905 (=*Galliaetatus* Ameghino, 1905). Medial Oligocene-medial Miocene, Europe.
  - *Manis* Linnaeus, 1758 (=and/or includes *Pholidotus* Brisson, 1762; *Pangolinus* Rafinesque, 1821; *Phataginus* Rafinesque, 1821; *Phatages* Sundevall, 1843; *Smutsia* Gray, 1865; *Paramanis* Pocock, 1924; *Uromanis* Pocock, 1924). Pleistocene, Europe; Pleistocene-Recent, Asia; Recent, Africa.

?PHOLIDOTA, *incertae sedis*
- *Tubulodon* Jepsen, 1932. Early Eocene, North America.

REFERENCES

Abel, Othenio
1922. Lebensbilder aus der Tierwelt der Vorzeit. Jena, Gustav Fischer, vii+643 pp., 507 figs.

Ameghino, Florentino
1904. Nuevas especies de mamíferos, cretáceos y terciarios de la Republica Argentina. An. Soc. Cient. Argentina, Buenos Aires, vols. 56–58, pp. 1–142.
1905. Les édentés fossiles de France et d'Allemagne. An. Mus. Nac. Buenos Aires, vol. 13, pp. 175–250.
1908. Encores quelques mots sur les tatous fossiles de France et d'Allemagne. *Ibid.*, vol. 17, pp. 104–106.

Brisson, Mathurin Jacques
1762. Regnum animale in classes IX distributum sive synopsis methodica. Editio altera auctior. Leiden, Theodorum Haak, viii+296 pp.

Colbert, Edwin H.
1942. An edentate from the Oligocene of Wyoming. Notulae Nat., vol. 109, 16 pp., 8 figs.

CUVIER, GEORGES L. C. F. D.
1800. Leçons d'anatomie comparé. Paris, Bauduin, vol. 1, xxxi+521 pp.

DEHM, RICHARD
1937. Neue Tertiäre Spaltenfüllungen im südlichen Fränkischen Jura (Vorläufige Mitteilung). Centralbl. Min. Geol. Palaeont., Abt. B, 1937, pp. 349–369.

DOUGLASS, EARLE
1905. The Tertiary of Montana. Mem. Carnegie Mus., vol. 2, pp. 203–224, figs. 13–16, pl. 22.

DUBOIS, E.
1907. Eenige von Nederlandschen kant verkregen uitkomsten met betrekking tot de kennis der Kĕndeng-Fauna (Fauna van Trinil). Tijdschr. K. Nederlandsch Aardr. Genootsch., ser. 2, vol. 24, pp. 449–458.
1908. Das geologische Alter der Kendeng oder Trinil-Fauna. *Ibid.*, ser. 2, vol. 25, pp. 553–555.
1926. *Manis palaeojavanica*, the giant pangolin of the Kendeng fauna. Proc. K. Akad. van Wetensch. Amsterdam, vol. 29, no. 9.

EVERNDEN, J. F., D. E. SAVAGE, G. H. CURTIS, AND G. T. JAMES
1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. Amer. Jour. Sci., vol. 262, pp. 145–198, 1 fig.

FILHOL, M. H.
1894. Observations concernant quelques mammifères fossiles nouveaux du Quercy. Ann. Soc. Nat. Zool., ser. 7, vol. 16, pp. 129–150, 21 figs.

FLOWER, WILLIAM HENRY
1882. On the mutual affinities of the Edentata. Proc. Zool. Soc. London, pp. 358–367.

FRECHKOP, SERGE
1931. Notes sur les mammifères. VI. Quelques observations sur la classification des pangolins (Manidae). Bull. Mus. Roy. Hist. Nat. Belgique, vol. 7, no. 22, pp. 1–14.
1949. Notes sur les mammifères. XXXVI. Explication biologique, fourni par les tatous, d'un des charactères distinctifs des xénarthres et d'un charactère adaptif analogue chez les pangolins. Bull. Inst. Roy. Sci. Nat. Belgique, vol. 25, no. 28, pp. 1–12, 9 figs.
1950. La locomotion et la structure des tatous et des pangolins. Ann. Soc. Zool. Belgique, vol. 80, pp. 5–8.

FRIANT, M.
1960. Morphologie et développement du cerveau des mammifères eutherians. IV. Séries des rongeurs, des pangolins et des l'oryctérope. Bull. Soc. Zool. Belgique, vol. 89, 1958–1959 [1960], pp. 365–394, 14 figs.

GALTON, JOHN CHARLES
1870. The muscles of the fore and hind limbs in *Dasypus sexcinctus*. Trans. Linnean Soc. London, vol. 26, pp. 523–565, 1 pl.

GAZIN, CHARLES LEWIS
1952. The lower Eocene Knight formation of western Wyoming and its mammalian faunas. Smithsonian Misc. Coll., vol. 117, no. 18, pp. 1–82, 6 figs., 11 pls.

GEOFFROY SAINT-HILAIRE, ETIENNE, AND GEORGES CUVIER
1795. Mémoire sur une nouvelle division des mammifères, et sur les principes qui doivent servir de base dans cette sorte de travail. Magasin encyclopédique, Paris, Millin, Noel et Warens, vol. 2, pp. 164–190.

GILL, THEODORE
1910. Classification of the edentates. Science, new ser., vol. 32, no. 810, p. 56.

GRAY, JOHN EDWARD
1821. On the natural arrangement of vertebrose animals. London Med. Repository, vol. 15, pt. 1, pp. 296–310.
1865. Revision of the genera and species of entomophagous Edentata, founded on the examination of the specimens in the British Museum. Proc. Zool. Soc. London, pp. 359–386, pls. 17–19.

GREGORY, WILLIAM KING
1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 332–341.

GUTH, CHRISTIAN
1958. Pholidota. *In* Piveteau, Jean, Traité de Paléontologie. Paris, Masson, vol. 6, no. 2, pp. 641–647, 8 figs.

GUTHRIE, DANIEL A.
1967. The mammalian faunas of the Lysite member, Wind River formation (early Eocene) of Wyoming. Mem. Southern California Acad. Sci., vol. 5, pp. 1–53.

HARRISSON, TOM, DIRK ALBERT HOOIJER, AND LORD MEDWAY
1961. An extinct giant pangolin and associated mammals from Niah Cave, Sarawak. Nature, vol. 189, no. 4759, p. 166.

HELBING, HERMANN
1938. Nachweis manisartiger Säugetiere im stratifizierten europäischen Oligocaen. Eclog. Geol. Helvetiae, vol. 31, pp. 296–303, 4 figs.

HOFFSTETTER, R.
1956. Caractères ancestraux et phylogenie des édentés xénarthres: 87–99. Colloq. Int. Cent. Nat. Rech. Sci., vol. 60, Problèmes actuels de paléontologie, pp. 1–163.

HOOIJER, DIRK ALBERT
1947. A femur of *palaeojavanica* Dubois from western Java. Proc. K. Nederlandisch

Akad. Wetensch., vol. 50, pp. 413–418, 1 pl.
1961. The giant extinct pangolin (*Manis palaeojavanica* Dubois) from Niah. Sarawak Mus. Jour., vol. 9, pp. 350–355, 1 pl.

HUMPHRY, G. M.
1870. The myology of the limbs of the Unau, the Aï, the two-toed anteater, and the pangolin. Jour. Anat. Physiol., vol. 4, pp. 17–78, pls. 1–4.

HUXLEY, THOMAS HENRY
1872. A manual of the anatomy of vertebrated animals. New York, D. Appleton and Co., 431 pp.

JEPSEN, GLENN
1932. *Tubulodon taylori*, a Wind River Eocene tubulidentate from Wyoming. Proc. Amer. Phil. Soc., vol. 71, pp. 255–274, 1 fig., 1 pl.

JOLLIE, MALCOLM
1968. The head skeleton of a new-born *Manis javanica* with comments on the ontogeny and phylogeny of the mammal head skeleton. Acta Zool., vol. 49, pp. 227–305, figs. 1–15.

KORMOS, THEODOR
1934. *Manis hungrarica*, n. sp., des erste Schuppentier aus dem europäischen Oberpliozän. Folia Zool. Hydrobiol., vol. 6, pp. 87–94, 1 pl.

LINNAEUS, CAROLUS
1758. Systema naturae. Editio decima, reformata. Stockholm, Laurentii Salvii, vol. 1, [ii]+824 pp.

LYDEKKER, R.
1886. The fauna of the Carnul caves. Mem. Geol. Surv. India, Palaeont. Indica, ser. 10, vol. 4, pt. 2, pp. 23–58, 1 fig., pls. 7–11.

MATTHEW, W. D.
1906. Fossil Chrysochloridae in North America. Science, new ser., vol. 24, no. 624, pp. 786–788.
1912. Ancestry of the edentates. Amer. Mus. Jour., vol. 12, pp. 300–303.
1918. Edentata. *In* Matthew, W. D., and W. Granger, A revision of the lower Eocene Wasatch and Wind River faunas. Part V—Insectivora (continued), Glires, Edentata. Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 565–657, figs. 1–68.
1928. *Xenotherium*, an edentate. Jour. Mammal., vol. 9, pp. 70–71.

OSBORN, HENRY FAIRFIELD
1904. An armadillo from the middle Eocene (Bridger) of North America. Bull. Amer. Mus. Nat. Hist., vol. 20, pp. 163–165.

PARKER, W. K.
1885. On the structure and development of the skull in Mammalia. Part II. Edentata. Phil. Trans. Roy. Soc. London, 1885, pt. 1, pp. 1–119.

POCOCK, ROYAL I.
1924. The external characters of the pangolins (Manidae). Proc. Zool. Soc. London, pp. 707–723.

QUENSTEDT, F. A.
1885. Handbuch der Petrefaktenkunde, 4th ed., 2 vols., Tübingen, Verlag der H. Laupp'schen Buchhandlung, 1239 pp., 443 figs., 100 pls.

RAFINESQUE, CONSTANTINE SAMUEL
1821. Sur le genre *Manis* et description d'une nouvelle espèce: *Manis ceonyx*. Ann. Gén. Sci. Phys. Bruxelles, vol. 7, pp. 214–215.

RÖSE, C.
1892. Ueber rudimentäre Zahnanlagen der Gattung *Manis*. Anat. Anz., vol. 7, pp. 618–622.

SCHLOSSER, MAX
1904. Notizen über einige Saügethierfaunen aus dem Miocän von Würtemberg und Bayern. Neues Jahrb., Beil.-Bd., vol. 19, pp. 485–502, pl. 26.
1907. Review of Ameghino, 1905. Neues Jahrb., pt. 1, pp. 462–466.
1923. Grundzüge der Paläontologie (Paläozoologie) von Karl A. von Zittel. II Abteilung—Vertebrata. Neuarbeitet von F. Broili und M. Schlosser. Munich and Berlin, R. Oldenbourg, v+706 pp.

SCOTT, WILLIAM BERRYMAN
1913. A history of land mammals in the western hemisphere. New York, The Macmillan Co., xiv+693 pp.

SHRIVASTAVA, R. K.
1963. Deltoid musculature of the Edentata, Pholidota, and Tubulidentata. Okajimas Folia Anat. Japan, vol. 38, pp. 25–38, 5 figs.

SIMPSON, GEORGE GAYLORD
1927. A North American Oligocene edentate. Ann. Carnegie Mus., vol. 17, no. 2, pp. 283–298, pl. 24.
1931. *Metacheiromys* and the relationships of the Edentata. Bull. Amer. Mus. Nat. Hist., vol. 59, art. 6, pp. 295–381, 23 figs.
1945. The principles of classification and a classification of mammals. *Ibid.*, vol. 85, xvi+350 pp.
1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. Amer., vol. 58, pp. 613–688, 6 figs.
1948. The beginning of the age of mammals in South America. Part I. Introduction, Systematics: Marsupialia, Edentata, Condylarthra, Litopterna, and Notioprogonia. Bull. Amer. Mus. Nat. Hist., vol. 91, pp. 1–232, 80 figs., 10 pls.
1959. A new middle Eocene edentate from

Wyoming. Amer. Mus. Novitates, no. 1957, 22 pp., illus.

STARCK, D.
1940. Über die rudimentären Zahnanlagen und einige weitere Besonderheiten der Mundhöhle von *Manis javanica*. Anat. Anz., vol. 89, pp. 305–315, 6 figs.
1941. Zur morphologie des Primordialkraniums von *Manis javanica* Desmaret. Gegenbaurs Jahrb., vol. 86, pp. 1–122, 47 figs.

SUNDEVALL
1843. K. Vet.-Akad., Handl., vol. 63, pp. 245–281.

TURNER, H. N., JR.
1851. On the arrangement of the edentate Mammalia. Proc. Zool. Soc. London, no. 19, pp. 205–221.

VAN DER KLAAUW, C. J.
1931. The auditory bulla in some fossil mammals with a general introduction to this region of the skull. Bull. Amer. Mus. Nat. Hist., vol. 62, pp. 1–352, 18 figs.

VIRET, JEAN
1951. Catalogue critique de la faune des mammifères miocènes de la Grive Saint-Alban (Isére). Première partie: Chiroptères, carnivores, édentés, pholidotes. Nouv. Arch. Mus. Hist. Nat. Lyon, no. 3, pp. 3–104, 23 figs., 4 pls.
1955. Ordre des pholidotes. Formes fossiles. *In* Grassé, Pierre-P. (ed.), Traité de Zoologie. Paris, Masson, vol. 17, no. 2, pp. 1283–1284, fig. 1224.

VON KOENIGSWALD, W.
1969. Die Maniden (Pholidota, Mamm.) des europäischen Tertiärs. Mitt. Bayer. Staatssamml. Paläont. Hist. Geol., vol. 9, pp. 61–71, 9 figs.

WEBER, MAX
1891. Beiträge zur Anatomie und Entwicklung des genus *Manis*. *In* Weber, Max, Zoologische Ergebnisse eine Reise in Niederlandish Ost-Indien. Leiden, E. J. Brill, vol. 2, pp. 1–116, pls. 1–9.
1904. Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. Jena, Gustav Fischer, xii+866 pp.

WINDLE, B. G., AND F. G. PARSONS
1899. Myology of the Edentata. Proc. Zool. Soc. London, pp. 314–338, 990–1017.

WINGE, HERLUF
1915. Jordfundne og nulevende Gumlere (Edentata) fra Lagoa Santa, Minas Geraes, Brasilien. Copenhagen, Mus. Lundii, vol. 3, no. 2, pp. 1–321, pls. 1–42.
1923. Pattedyr-Slaegter. Copenhagen, H. Hagerups Forlag, vol. 1, Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata, vii+360 pp., 1 pl.

WORTMAN, J. L.
1897. The Ganodonta and their relationship to the Edentata. Bull. Amer. Mus. Nat. Hist., vol. 9, pp. 59–110.
1903. Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum. Part II. Primates. Suborder Cheiromyoidea. Amer. Jour. Sci., ser. 4, vol. 15, pp. 163–176, 399–414, 419–436; vol. 16, pp. 345–368, pls. 11–12.

ZDANSKY, OTTO
1926. Über der systematische Stellung von *Xenotherium* Douglass. Bull. Geol. Inst. Uppsala, vol. 20, pp. 231–236, figs. 1–3.